Taphonomic analysis of the MIS 4–3 (Late Pleistocene) faunal assemblage of Biśnik Cave, Southern Poland: Signs of a human-generated depot of naturally shed cervid antlers?

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ABSTRACT

The present is a palaeobiological and taphonomic analysis of a Marine Isotope Stages (MIS) 4–3 (Late Pleistocene) assemblage of animal remains and hominin artefacts from layers 7–5 of Biśnik Cave, Częstochowa Upland, Poland. The analysis indicates that the bone assemblage is the result of a time-averaged palimpsest of both biotic and episodic abiotic events, the former consisting of many successive generations of animals and hominins that frequented the cave, and the latter including hydraulic winnowing. In fact, the taphonomic history of the fossil assemblage from Biśnik Cave's layers 7–5 is partially obscured by the overprint of hydraulic winnowing, which purportedly removed a certain amount of the original specimens. Besides evidence of cave bear deaths from non-violent, hibernation-related mortality and of occupation by generations of denning wolves and hyaenas, there is a wealth of flint artefacts, alongside remains of a few fireplaces and of a structure built in the cave by hominins to partition the cave chambers. The studied layer contains an impressive number of shed antlers, primarily of the red deer *Cervus elaphus*. *Crocuta crocuta spelaea* is normally held responsible for such accumulations of shed antlers in various European caves; Biśnik Cave's layers 7–5 will therefore simply add to the list. However, the role of accumulator of shed antlers attributed to the Pleistocene spotted hyena does not match the behaviour of its modern counterpart and seems not accounted for metabolically. The only reasonable alternative is that the antlers were collected by hominins. From this alternative perspective the cave would have functioned as a warehouse, where naturally shed antlers were stored as raw material, potentially to be shaped into tools and/or employed as tools to make other tools. The palaeobiological and taphonomic analysis presented here provides new insights into the succession of pre- and postdepositional events that involved the bone remains accumulated in the cave, as well as into the interactions between the animals and hominins of the time. More importantly, if hominins, and not hyaenas, were responsible for the amassment of the shed antlers in Biśnik Cave, this study raises doubts as to the hyaenid or human origin of other similar cave accumulations of shed antlers throughout Europe.

1. Introduction

Biśnik Cave is renowned among archaeologists for its rich record of prehistoric evidence spanning from the early Middle Pleistocene on. Interdisciplinary research of the cave started in 1992. The special interest for this site lies in its sediment sequences which span the last 300,000 years. It contains evidence of seventeen Palaeolithic cultural levels and of the earliest presence of Neanderthals in Poland (Cyrek et al., 2010; Cyrek, 2013 and references therein), framed in the context of the climate and environmental changes recorded by the deposits.

Microstratigraphic analysis permitted the detailed identification of sub-levels as well as of different phases of use of the cave in each layer, during either warm or cold episodes (Cyrek et al., 2014). Biśnik Cave records the main cultural Middle Palaeolithic transitions in Polish Jura and is located at a crucial, central European crossroads for faunal and hominin migrations; this makes it a key site for the modelling of Quaternary climate change.

The layers 7–5 in Biśnik Cave's sequence document events at the MIS 4–3 transition. They yielded 1407 Middle Palaeolithic Micoquian artefacts, from two distinct levels; they form the largest known collection of its kind from a cave site. Levallois methods were used to produce semi-products of the tools: knives and side-scrapers. Some of the tools were made using the bifacial method (Cyrek et al., 2014 and references therein). Because of the special attention received by Biśnik Cave's layers 7–5, in this article we present an overview of the taphonomic processes that operated at the time of their deposition, with more in-depth coverage given to particular aspects that emerged from the analysis. This study was conducted not only with the aim of providing a detailed description and illustration of the taphonomic signatures exhibited by the faunal remains associated with the lithic industry, but also with the intent to unlock information needed to reveal possible decisions adopted by the humans during the site's occupational phase,

thereby reflecting possible cultural behaviours. The archaeological and palaeontological assemblage from layers 7–5 is in fact ideally suited for careful palaeobiological and taphonomic analyses; nonetheless, it is a complex accumulation, the result of multiple taphonomic pathways, and consequently does not fit into the common taphonomic schemes.

2. Cave location, sequence description and palaeontology

2.1. Biśnik Cave

Biśnik Cave (50°25′35.42″N 19°39′56.03″E) is located in the region of the Smoleń-Niegownice range, in the southern part of the Częstochowa Upland and opens on the Wodąca Valley (Fig. 1A and B). The cave consists of two chambers, a main one and a side one, a side shelter, an area located under the overhang and two entrances (Figs. 1C and 2). Biśnik Cave contains one of the most complete sequences of cave deposits of all the central Polish Jura. The stratigraphic succession spans the upper Middle Pleistocene to the whole Upper Pleistocene, and therefore correlates with the Marine Isotope Stages (MIS) 8–2. It includes more than 20 Middle and Upper Pleistocene and Holocene sedimentary events, with more than a dozen different types of cultural variants, at different states of preservation (Cyrek, 2009, 2013; Cyrek
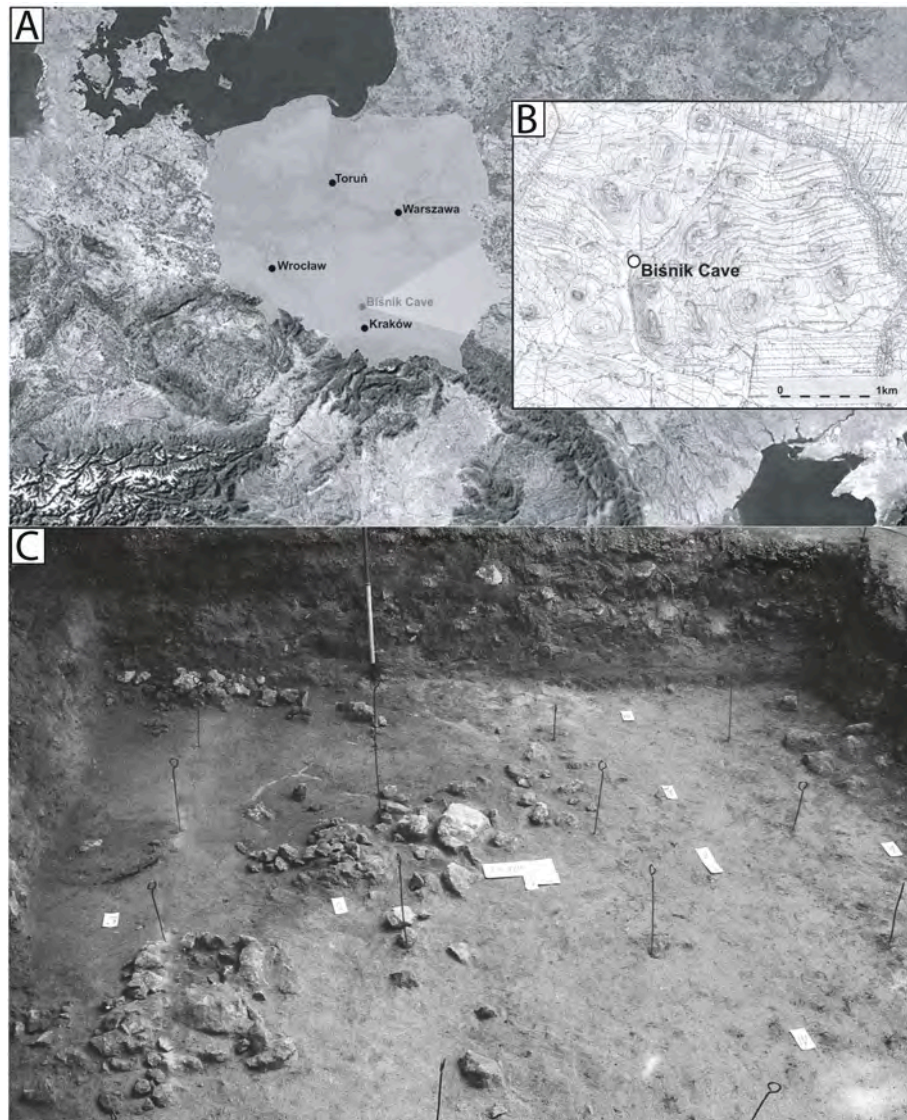
Fig. 1. Location of the site. A) Geographical location of Biśnik Cave in Poland. B) Detailed location of the cave. C) Photo of the stone structure.
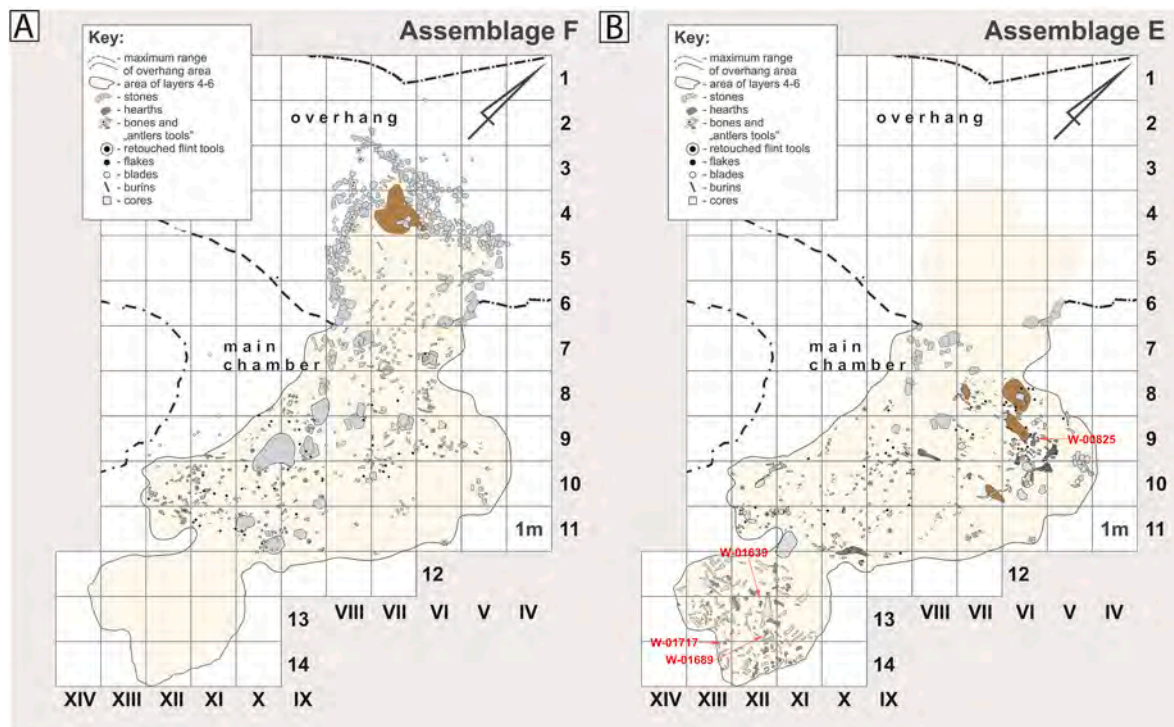
Fig. 2. Spatial arrangement of the lithic implements. A) Biśnik Cave's layers 7-5 plan. Map of all categories of specimens of Assemblage F. B) Detail of the stone structure plan. Map of all categories of specimens of Assemblage E. Red arrows indicate the location, and red labels the inventory numbers, of the shed antlers with evidence of hominin modifications. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

et al., 2010, 2014; Krajcarz et al., 2014a, 2016). With its vertically stacked sequence of Middle Palaeolithic industries that prove the unequivocal presence of hominins in virtually all its layers, Biśnik Cave is an unprecedented example in the area of repeated human occupancy (Fig. 3).

The cave was first explored back in 1991 and excavations have so far been conducted fairly regularly. This led to the recovery of several hundred thousand animal bones, as well as of over 4000 stone, bone and horn/antler tools. The cave therefore offers the unique opportunity to frame the long hominin occupation within the environmental changes that occurred over a time period of 400 000 years.

2.2. Stratigraphy and chronology

The cave's stratigraphic succession (Fig. 3) includes three groups of deposits, 20 layers each, of different colour, grain-size, geometry, thickness and lithologic and mineralogical composition (Mirosław-Grabowska, 2002a, b; Krajcarz et al., 2014a). All layers were dated using thermoluminescence (TL) and optically stimulated luminescence (OSL) methods, and bones from the youngest layers (6–1) were dated with the Accelerator mass spectrometry radiocarbon method (Krajcarz et al., 2014a). The lowermost layers, from the base to layer 8, are thick, continuous, with fairly high clay and low silt and sand contents. Layer 16 is OSL-dated to 159.0 ± 9.2 ka, and layer 12 is TL-dated between 102.0 ± 15.0 and 93.0 ± 15.0 and OSL-dated between 116.9 ± 11.8 and 88.9 ± 5.1 ka (Krajcarz et al., 2014a). Over layer 8, with the interposition of elements derived from a partial collapse of the cave ceiling caused by the action of running water, lie the loamy sands of layers 7–5, which provided the fossil material object of the present study. Layer 7 is TL-dated between 71.0 ± 7.4 and 64.6 ± 6.5 ka and OSL-dated between 69.8 ± 3.9 and 62.1 ± 3.6 ka; radiocarbon-dated bones collected from layers 6-5 gave calibrated ages ranging from 51.280 to 42.949 years BP (Krajcarz et al., 2014a). In the main chamber of the cave the 7-5 section is from 1 m to 2.5 m thick. Micro-morphological analysis revealed that it is largely formed by

allochthonous sediments introduced into the cave during episodic flash-flood events from the Wodąca Valley. Animals and hominins frequented the cave during breaks between these events.

Layers 7–5 are the upper portion of a laminated sand to loess sequence (Fig. 3). They deposited over an erosive surface, created by streaming water that truncated a section of older sediments. This episode occurred in the Interplenivistulian (MIS 4–3).

Layers 4–2 are sand, loess and loess-like silty sediments of aeolian origin, radiocarbon-dated from 36.355 to 11.354 years BP (Krajcarz et al., 2014a). Finally, layer 1 consists of light-brown loam and dark-grey sandy loam, radiocarbon-dated 24.531–5.030 years BP and OSL-dated 14.0 ± 1.3 ka (Krajcarz et al., 2014a).

2.3. Cultural evidence

Culturally, layers 7 and 5 contain evidence of two following episodes of human occupation. These are clearly indicated by the presence of fireplaces, by the prevalence of semi-product and cores over tools, which indicates in-situ stone-tool manufacturing and by an inner wall partitioning the habitation zones (Fig. 1C; Assemblages E and F in Fig. 2; Cyrek et al., 2010, 2014). The lithics include uni- and bi-facial knives, as well as implements obtained with the use of Levallois technology, which dominates over the discoid flaking technique.

The older cultural level (Assemblage E: Fig. 2B) was contained in layer 7; it includes flint samples and the 51 naturally shed deer antlers, which were processed around hearths located in the main chamber of the cave, next to the entrance; smaller, closely spaced concentrations of charcoal are present inside the main chamber, associated with sparse stone artefacts (Fig. 2). The flint assemblage, which consists of 270 objects, was made in the Levallois technique. The tools are dominated by side scrapers and bifacial knives of Micoquian character (Cyrek et al., 2010, 2014). The assemblage includes almost all the red deer antlers included in the sample for the present study. A use-wear (traceological) analysis performed on several knives found evidence suggestive of use for processing antler or wood (Cyrek et al., 2014). In the light of the
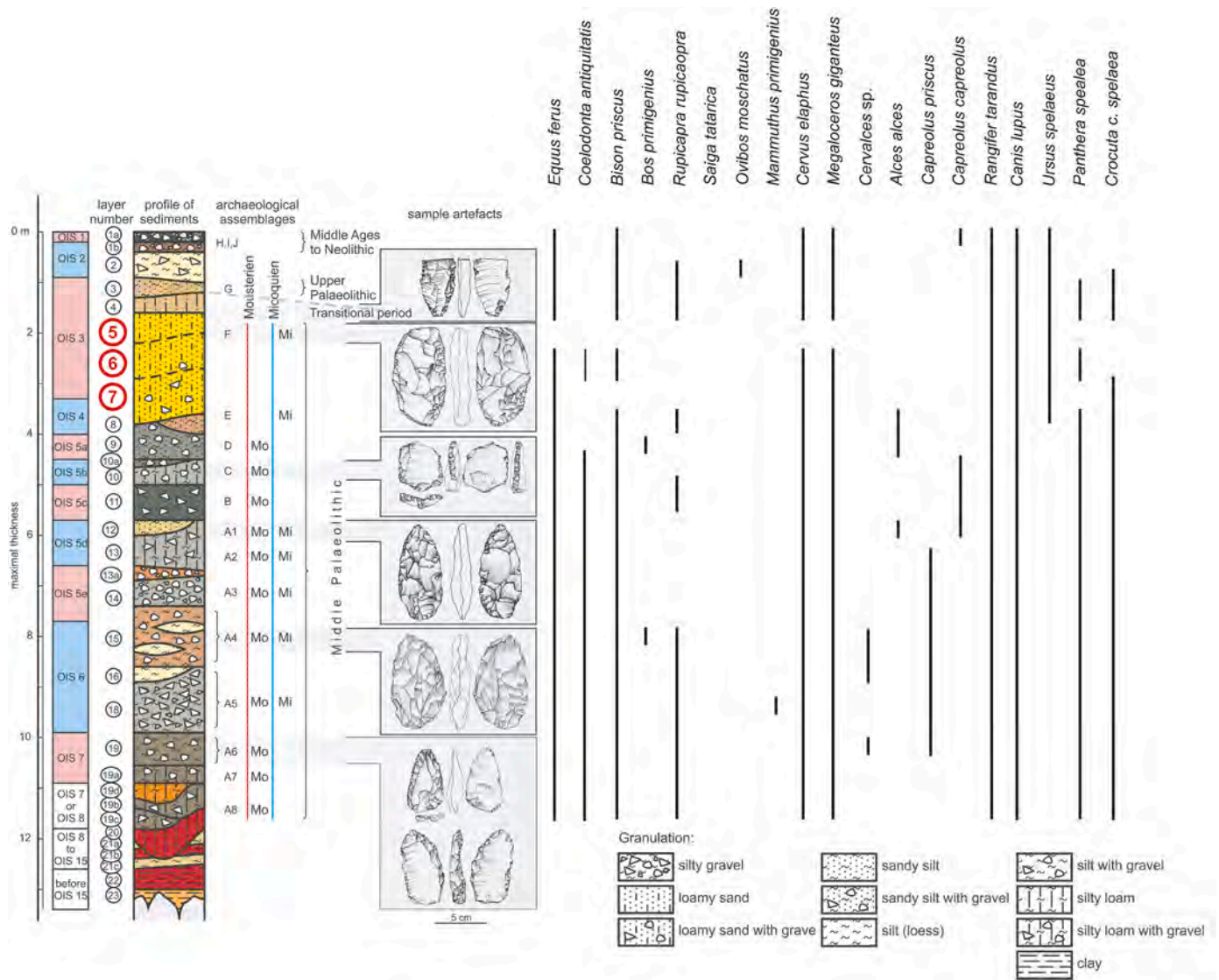
Fig. 3. Biśnik Cave's stratigraphic log, vertical distribution of the stone tools found in the cave and range chart of the taxa. Some of them, such as *Equus ferus*, *Bison priscus*, *Cervus elaphus*, *Megaloceros giganteus*, *Rangifer tarandus*, *Canis lupus* and *Crocuta crocuta spelaea*, are distributed throughout the whole stratigraphic succession.

results of the present study, it is reasonable to relate this evidence to the treatment of deer antlers.

A second phase of occupation, attested to in layer 5, is evidenced by a younger cultural level (Assemblage F: Fig. 2A), connected with the construction of an irregular, semi-circle wall of gravel and rare large bones. Series of stone, all of peculiar size and height, were found arranged in oval clusters. They were apparently placed around vertical construction poles. The enclosed area was filled with some 25 cm of sediment and the preserved wall surrounding it was c.a. 30 cm high. A strip of brown sand, most likely the residue of an original wall made of organic material, lied directly under the stone wall for all its extension. The structure was built in front of the cave entrance, under the overhang, around a grey, loess-sandy deposit containing a concentration of cultural remains (Figs. 1C and 2B: Cyrek, 2002, 2003; Cyrek et al., 2014). This is the oldest habitation structure in Poland. Evidence of a possible bone-fuelled hearth was found in the NE part of the structure. Next to it, a gap in the stone wall, with vertebrae of large-size animals on both sides, possibly marked a passageway into the structure. Chemical analysis of ground samples revealed over a dozen times higher concentrations of phosphorus, organic coal and humus inside the structure than outside it, in its close vicinity (Cyrek, 2002). The sediment filling the enclosure contained the same kinds of flint artefacts and bone

fragments found in layer 5 under the overhang; a small cluster of these elements was present around the hearth, whereas a larger concentration was found at the entrance to the main chamber. The 1137 Assemblage F flint artefacts had Micoquian cultural typologies, very similar to those of Assemblage E (Cyrek et al., 2010, 2014). The suite of stone artefacts found here includes initial cores, unfinished bifacials, finished to vestigial and repaired tools. The entity and structure of the assemblage indicates that the cave was used as a long-term campsite, where many different activities were carried out. The irregular wall is the oldest dwelling construction (or windscreen?) known in Poland (Cyrek, 2003). Several other similar constructions made using stones and animal bones are known from other Middle Palaeolithic European sites. Some of them are reported from caves, i.e., Lazaret, La Baume des Peyards, Combe Grenal (Kozłowski, 2004), and others from open sites, i.e., Orgnac 3, Becov (Kozłowski, 2004), Bilzingsleben (Mania, 2004). One was also found at Poitiers "La Folie" (Bourguignon et al., 2002). They are interpreted either as dwelling structures, or as defences against wind or animal intrusion.

2.4. Palaeontological overview

The distribution of the taxa through the different deposits of Biśnik

Cave is depicted in Fig. 3. Layers 19a-d and 18 date to MIS 9–8 (Mirosław-Grabowska, 2002a, b) or to MIS 7 (Krajcarz et al., 2014a). They yielded remains of *Equus ferus, Coelodonta antiquitatis, Sus scrofa, Bison priscus, Rupicapra rupicapra, Cervus elaphus, Capreolus priscus, Rangifer tarandus, Cervalces* sp., *Megaloceros giganteus, Canis lupus, Panthera spelaea* and *Crocuta crocuta spelaea. Mammuthus primigenius* is hardly represented in layer 18. Small mammal assemblages indicate that layer 19 deposited during a warm phase of MIS 8 and layer 18 formed during an even warmer climatic optimum of MIS 7 (Socha, 2014).

Layers 16 and 15 are dated to MIS 7 or MIS 6. *Bos primigenius* adds to the bovid species seen above, while slight changes at the subspecies level are shown by prominent representatives of the cervid group (*Cervus elaphus spelaeus, Megaloceros giganteus antecendens/germaniae*). *Cervalces* sp. is represented here for the last time. Small mammals indicate that these layers accumulated at a time of warm temperatures, but not as high as those that characterized the Eemian optimum (Socha, 2014).

Layers 14 and 13 correlate with the warm MIS 5e (former Eemian Interglacial), as also confirmed by the micromammal remains found in them (Socha, 2014). Ungulates grow more abundant but lose the aurochs and the chamois. The two latter species appear again in the section bracketing layers 12–9, the modern elk *Alces alces* makes its first appearance in layer 12, where in fact small mammals indicate a deterioration of climate (Socha, 2014), and the red deer and the giant deer are represented by new subspecies, *Cervus elaphus simplicidens* and *Megaloceros giganteus garmaniae/ruffi*, respectively. Paleoclimate proxies delineate more dynamic conditions moving upwards from layer 12 through the succession (Socha, 2014). The cold glacial cycle MIS 4 is documented in layer 8. The chamois appears again. The cave bear makes its first appearance at the transition from layer 8 to layer 7 and will stably persist thereafter. Skipping the faunal occurrences from layers 7–5, which are the subject of the present analysis, the next noteworthy faunal events are contained in a set of layers (5–3) that date from the MIS 3 interglacial to the early MIS 2 glacial. Small mammal evidence points to a gradual deterioration of climatic conditions, leading to the very cold end of MIS 3 (Socha, 2014). The saiga antelope appears for the first - and only - time in cave's deposits, and there is a second, spot occurrence of the musk-ox.

Cooling climatic conditions and grass-dominated steppe landscapes that progressively increase, typical of the end of the Middle Pleniglacial (Interplenivistulian), at the MIS 3–2 transition, are indicated in layers 3-2 by a varied small mammal community including the pika, the lemming and the narrow-headed vole, together with the edible dormouse, the birch mouse, and several murids. The steadily deteriorating conditions cause the disappearance of *Panthera spelaea*. Layers 3-2 document also the transition to the Last Glacial Maximum (MIS 2).

Layers 2 to 1 deposited at a time of climate improvement (Socha, 2014). The effects of the climatic amelioration are recorded in layers 1/2-1a and b by the disappearance of late Pleistocene, cryophilic taxa and the appearance of Holocene ones. During the Holocene, Pleistocene holdovers become extinct.

A new appearance of the modern elk in sites located in the surroundings of the cave, presumably at the beginning of the Holocene, is assumed to indicate moist biotopes. At this time, parkland and woodland mammals, such as the European bison, the aurochs, the red deer, the roe deer and the wild boar become dominant in the area. Finally, the appearance of sparse remains of domesticated animals, such as cattle, sheep, goat and probably swine and horse in the Holocene layers of Biśnik Cave record the first settlement of agricultural people in the Wodąca Valley (Stefaniak and Marciszak, 2009; Marciszak and Stefaniak, 2010; Van Asperen and Stefaniak, 2011; Marciszak et al., 2011ba; Croitor et al., 2014; Krajcarz et al., 2014b; Marciszak, 2014; Piskorska and Stefaniak, 2014; Van der Made et al., 2014; Socha, 2014; Stefaniak, 2015).

3. Materials and methods

Biśnik Cave yielded a wealth of fossils over the years. This unique collection of bones is housed in the Department of Palaeozoology of the Institute of Environmental Biology of the University of Wrocław. Flint artefacts, bone remains and research documentation are kept at the Chair of Environmental Archaeology and Human Palaeoecology, Institute of Archaeology of the Nicolaus Copernicus University in Toruń.

Because the intended task of this study was to illustrate the complexity of the overall taphonomic processes that had been involved over the whole period of formation of Biśnik's layers 7–5, the analysis was targeted at the palaeobiological and taphonomic information embedded in the bulk of the sample from all three layers; specific aspects in individual layers were explored more in-depth when necessary. The study started with the identification of the specimens, when possible both anatomically and taxonomically. The identifiable fraction of the total assemblage retrieved from the 7–5 level was then tallied to produce the number of identified specimens (NISP), the minimum number of individuals (MNI) and the minimum number of elements (MNE). MNIs and MNEs were estimated using a comprehensive method which attributed to single individuals as well as to single elements, respectively, by side-matching, taking into account size, proportions, age, degree of ossification, and, when possible, sex (de Ruiter, 2004; Lyman, 2008, 2018). The state of preservation and the type and intensity of bone modification have also been considered for these quantifications.

The analysis was extended to include the 7–5 faunal assemblage exceeding 50 kg, which comes from a relatively confined area of the cave and from a single depositional unit; in this way the effects of aggregation as well as those of the context had no effects on the estimation of the MNI counts. The skeletal representation was assessed by comparing the observed versus MNI-based expected frequencies (i.e., expected amounts were obtained multiplying the number of times an i-element occurs in a skeleton of that given taxon by the MNI counts for that taxon).

Binford's (1978) minimal animal unit, MAU, was also used for measuring the frequency of skeletal parts. MAU values were calculated by dividing the MNE counts by the number of times each skeletal part occurs in one skeleton. Then, MAU counts were normed and referred to as %MAU values by dividing them by the maximum MAU value in the assemblage.

3.1. Palaeobiological information

Specific palaeobiological information has been gleaned from a variety of sources. Several specimens were ontogenetically aged by long bone epiphyseal fusion, degree of ossification, antler development and, especially, tooth eruption and wear; teeth are less liable to biostratinomic damage than postcranial bones, and thereby provide fairly reliable indications of the age of animals at death. The age limitations for juveniles, subadults and adults, as well as the age-scoring techniques used here, i.e., eruption and wear schemes for different taxa based on both isolated and in situ cheek teeth, were drawn from the papers of various authors. These include: Spinage (1972), Miller (1974), Outram and Rowley-Conwy (1998), Domingo et al. (2018); Nacarino-Meneses et al. (2016, 2017) (for horses); Payne (1973), Grant (1982), Hufthammer (1995), Prins (1996), Enloe (1997), Gaudzinski and Roebroeks (2000), Hambleton (2001), Loison et al. (2001), Høymork and Reimers (2002), Hall (2005), Mysterud et al. (2007), Wallingford et al. (2017) (for bovids and cervids); Landon et al. (1998), Gipson et al. (2000), Stiner (2004) (wolves and hyaenas); Bunnell and Tait (1981), Wielgus and Bunnell (1994), Bernhoft et al. (1997), Mattson (1997), Norstrom et al. (1998), Stiner (1998), Friebe et al. (2001), Swenson et al. (2001), Gau et al. (2004), Dahle et al. (2006), Kaczensky et al. (2006), Elfström et al. (2008), Weinstock (2009), Graham et al. (2010), McLellan (2011), Debeljak (2014) (for bears).

3.2. Bone fragmentation

The intensity of fragmentation was assessed using Richardson's (1980) fragmentation index NISP:MNE, but also NISP:MNI, although both ratios do not indicate whether breakage was pre- or post-burial (Binford, 1981, 1984; Klein and Cruz-Uribe, 1984). The indexes were calculated for each species. Lyman (1994) warned that the inclusion of whole or complete bones in NISP and MNE counts lowers the ratio; for this reason, NISP:MNE ratios have been calculated without complete bones included in the tallies (and the same for the NISP counts in the NISP:MNI ratios), in order to determine to what degree bone fragments overlap each other, and therefore their grade of comminution.

The degree of fragmentation in the different taxa was also indirectly assessed using Marean's (1991) "completeness index" which is estimated on compact carpal and tarsal bones. It is calculated based on the sum of complete and fragmented specimens of each basipodial bone preserved for each taxon, divided by the total NISP counts for that bone and taxon and then multiplied by 100. The index is typically high (>92%) for sets of carpals and tarsals left over by carnivores.

An attempt was made to discriminate bone fractures that might have been produced at different stages in the taphonomic history of Biśnik Cave's 7–5 assemblage, that is, when the bones were still in fresh (green-bone, recently defleshed) state or when already dry. Reference for this was made to Haynes' (1983), and Villa and Mahieu's (1991) methodologies.

3.3. Susceptibility to fluvial transport

Because the 7–5 sandy sediments were brought in Biśnik Cave by water flooding in from the Wodąca Valley (Cyrek et al., 2010), special attention was given to the possible role played by water in the formation of the fossil assemblage from these layers. Skeletal elements are differentially transported, sorted by weight, and shape by streaming water action of sufficient intensity and duration differentially (Voorhies, 1969; Behrensmeyer, 1982; Aslan and Behrensmeyer, 1996). Smaller, lighter specimens are experimentally observed to move prior to larger, heavier ones (Voorhies, 1969; Behrensmeyer, 1975; Hanson, 1980). The Voorhies' approach (Voorhies, 1969; Behrensmeyer, 1975) was adopted to evaluate the susceptibility to fluvial transport of Biśnik Cave's individual, isolated remains of middle/small-size species. The saturated weight index (SWI: Todd and Frison, 1986:68; Lyman, 1994:174–176) was used to assess the relationship between bone weight and potential for water transport. This index is plotted against %MAU (minimum animal units; Binford, 1984) to determine how much an assemblage is modified by fluvial action (Todd and Frison, 1986:72). To investigate the %MAU/SWI relationships for some of the Biśnik Cave taxa, the SWI values reported by Behrensmeyer (1975) were used as the closest rough estimates available based on sizes/weights of the animals. Hence, the reindeer %MAU counts were plotted against the SWI values for topi antelopes, the wolf and hyaena %MAU data against the SWI values for reedbuck antelopes, and the bear %MAU values against the SWI values for zebra.

A further index of fluvial winnowing for mammalian deposits employed in this study is the tooth/vertebra ratio (T/V), proposed by Behrensmeyer (1975). In a live mammal skeleton the tooth/vertebra ratio normally approaches 1 (Badgley, 1986); teeth are the densest elements, whereas vertebrae are among the least dense ones. Moreover, given their high surface area to volume ratios, vertebrae are most readily transported by currents (Voorhies, 1969; Behrensmeyer, 1975). The higher the ratio, the more the deposit is winnowed; teeth therefore form the lag component and vertebrae the dispersed one of a winnowed skeleton.

3.4. Bone modification

A 14x and 10x hand lens and the criteria established by Behrensmeyer (1978), Blumenschine et al. (1996), Fisher (1995), Braun et al. (2008) and Cilli et al. (2000) were used to identify and categorise bone modifications, which were recorded in order to assess pre- and post-depositional alteration. Bones were assigned to one of the six weathering stages (WS) of progressive meteoric alteration (from stage 0 – non altered to stage 5 – heavily altered) described by Behrensmeyer (1978). Trampling (scratching, breaking), plant root/fungal/bacterial tunneling, corrosion, abrasion/polishing, carnivore-ravaging evidence (bites, punctures, scorings, gnawing marks, or gastric corrosion), alongside hominid-derived modifications (chopping marks, cut marks, drilling/hollowing out) were all recorded and summarised in bar graphs. The carnivore-inflicted chewing damage patterns were coded using Pobiner et al.'s (2020) Damage Levels 2, 3, and 4, where 2 = minimal chewing damage, 3 = moderate chewing damage, and 4 = severe chewing damage, fragmentation, or destruction.

3.5. Antler analysis

As already mentioned above, the excavations conducted over the years at Biśnik Cave have yielded a bounty of tools made from a wide variety of raw material types, including bone, horn and antler. The skeletal remains from Biśnik Cave's level 7-5 have therefore been subjected to special microscopic scrutiny to detect the presence, morphology, and patterns of distribution of human-derived modifications. Optical microscopic inspection was performed using a Nikon SMZ-745T microscope equipped with a DeltaPix Invenio 6EIII camera. The terminology employed to describe marks and alterations through microscopic examination follows that adopted in traceological and archaeological literature for osseous artefacts (e.g., Newcomer, 1974; d'Errico et al., 1984; Vaughan, 1985; van Gijn, 1989; Sidera, 1993; Jensen, 1994; Korobkova, 1999; Averbouh and Bodu 2002; Legrand, 2007; Osipowicz, 2010; Buc, 2011; Orłowska, 2016). The location, morphology and distribution of modifications detected on surfaces of the artefacts have been accurately recorded. Taphonomic analysis of the alterations of the bone tools was performed following standard procedures, in accordance with dedicated literature (e.g., Fisher, 1995; D'Errico and Villa, 1997; Jin and Shipman, 2010; Madgwick, 2014; Griffith et al., 2016).

4. Results

Biśnik Cave's three layers 7–5 yielded a total of 876 (identified specimens) fairly evenly distributed, subhorizontally deposited specimens, with the densities of bones decreasing northwards (Fig. 2, Table 1). The majority of the bones had bimodal NS/EW orientation. Isolated teeth and toothed mandible and skull fragments were found mostly concentrated in the main chamber of the cave. Coprolites were found in layer 7, gathered in two clusters, a larger one near the entrance of the cave and a smaller amount against the northern wall of the main chamber.

4.1. Palaeobiological information

In general, the fossil assemblage retrieved from layers 7–5 provided remains of at least 77 adults, 18 subadults, and 26 juveniles, pertaining to a total of 121 individuals (Table 1). Total NISP, MNE and MNI counts of the taxa, and the same counts ordered per layer (7–5, base to top of studied section), are summarised in Table 2; all cervid antlers are excluded from these counts. Overall, the taxa are represented by 2.66% of their preservable elements. The frequencies of the specimens, expressed in terms of NISP, MNE, MNI, MAU and %MAU counts, are displayed in Fig. 4 and reported in Tables 2 and 3. The total quantitative units show a notable dominance of *Ursus spelaeus* over all the other taxa; in fact, cave bears are particularly abundant in layer 7. Based on overall NISP values, *Ursus spelaeus* is followed in abundance by *Rangifer tarandus* and *Canis lupus*, and by *Canis lupus* and *Bison priscus* in terms of total

Table 1
Total quantitative amounts. NISP = Number of Identified Specimens; MNI = Minimum Number of Individuals; MNE = Minimum Number of Elements.

	NISP	MNI juveniles	MNI subadults	MNI adults	MNI total	MNE	MNI-based expected frequencies	Isolated teeth
Elephantidae	1	1	–	–	1	1	351	–
Rhinocerotidae	1	–	–	1	1	1	118	–
Coelodonta antiquitatis	12	–	–	2	2	10	236	2
Equus ferus	12	1	–	4	5	10	1025	5
Megaloceros giganteus	48	–	1	7	8	40	2616	9
Rangifer tarandus	127	2	1	7	10	52	1090	59
Cervus elaphus	85	1	1	8	10	19	3270	32
Bison priscus	84	1	2	5	8	66	1656	28
Canis lupus	96	2	1	5	8	71	2552	24
Ursus spelaeus	334	15	9	30	54	215	17226	212
Panthera spelaea	4	–	–	1	1	4	255	–
Crocuta crocuta spelaea	42	3	3	7	13	27	2509	22
Partial total	846	26	18	77	121	516	32904	393
Taxon indet	10	–	–	–	–	–	–	1
Anatom. Indet	13	–	–	–	–	–	–	–
Indet	7	–	–	–	–	–	–	–
Total	876	26	18	77	121	516	32904	394

Table 2
Quantitative amounts per layer. NISP = Number of Identified Specimens; MNI = Minimum Number of Individuals; MNE = Minimum Number of Elements.

	Layer 7			Layer 6			Layer 5		
	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI
Elephantidae	0	0	0	1	1	1	0	0	0
Rhinocerotidae	0	0	0	1	1	1	0	0	0
Coelodonta antiquitatis	0	0	0	12	10	2	0	0	0
Equus ferus	12	10	5	0	0	0	0	0	0
Megaloceros giganteus	0	0	0	48	40	8	0	0	0
Rangifer tarandus	41	10	3	45	24	3	41	18	4
Cervus elaphus	0	0	0	85	19	10	0	0	0
Bison priscus	0	0	0	84	66	8	0	0	0
Canis lupus	34	26	3	41	30	3	21	15	2
Ursus spelaeus	277	167	42	25	18	7	32	30	5
Panthera spelaea	0	0	0	4	4	1	0	0	0
Crocuta crocuta spelaea	42	27	13	0	0	0	0	0	0
Total	406	240	66	346	213	44	94	63	11

MNE counts. *Crocuta crocuta spelaea* is the second most abundant in the total MNI values, followed by *Cervus elaphus* and *Rangifer tarandus*; the hyaena, however, is present only in layer 7. Worth noting is that, by excluding shed and fragmental antlers from the units used to express the relative skeletal and taxon abundances, the only cervid distributed all through the studied section is the reindeer (Fig. 4, Table 2). In fact, *Cervus elaphus* and *Megaloceros giganteus* are represented in both layer 7 and 6, but, surprisingly, in layer 7 exclusively by antler remains.

4.2. Bone fragmentation

The NISP:MNE ratios reveal that remains of *Rangifer tarandus*, *Bison priscus*, *Ursus spelaeus*, *Canis lupus* and *Megaloceros giganteus* are the most fragmented of the assemblage, but the degree of breakage suffered by the bones of *Rangifer tarandus*, *Bison priscus* and *Canis lupus* is far higher than that of other taxa, relative to the respective MNI counts (Fig. 5). The fracture patterns indicate that, overall, there was no prevailing mode of breakage, as part of the limb bones were broken while still green and part when already dry (Fig. 6). At a more detailed level, however, the remains of *Bison* and *Coelodonta* were prevalently broken in a fresh state and virtually all of those of *Canis* and *Ursus* in a dry state.

The ontogenetic age, size, as well as structural density of bones influence their susceptibility to be fractured. Figs. 7 and 8 show that the assemblage is mainly formed by large, dense, well-ossified remains of adult individuals, to which belong all but two complete bones. Juveniles and subadults are largely - at times almost exclusively - represented by isolated teeth. So-called ''bone cylinders'', i.e., limb shafts that lack epiphyses but retain their original circumferences at least somewhere along their lengths, which would be frequent in hyaena-accumulated

faunal assemblages (Binford, 1981; Bunn, 1983; Todd and Rapson, 1988; Cruz-Uribe, 1991; Pickering, 2002; Kuhn et al., 2010), are only 7 in Biśnik Cave's 7–5 bone assemblage (Fig. 7, Fig. 9); in fact, they all come from layer 7, in association with the hyaena remains. Cruz-Uribe (1991) however warned that limb bones that were originally cylinders can be reduced to splinters by postdepositional processes such as sediment compaction and soil leaching; we should add that this can also be caused by praeburial processes such as trampling, or, in cave contexts, by postdepositional cave earth leaching.

4.3. Susceptibility to fluvial transport

At closer inspection we notice a strong and systematic underrepresentation of the vertebrae, ribcage elements, basipodial bones and phalanges in all the taxa (Figs. 10–12). On the other hand, cranial and dentognathic remains are comparatively more abundant. Isolated teeth form a conspicuous fraction of the bone assemblage, reaching a total of 394 (45%), which gives a T/V ratio of 8.38.

The underrepresented elements belong to the categories that experimental work has shown being relatively more susceptible to water transport (Fig. 13). This is also largely in line with the results of the % MAU/SWI relationships (Fig. 14). The Spearman rank correlation coefficients (p) indicate highly significant, positive correlation for *Canis* (0.46, p < 0.025), *Ursus* (0.65, p < 0.001) and *Crocuta* (0.87 p < 0.05). In contrast, the %MAU/SWI correlation is negative and not significant in *Rangifer* (0.07, p«0.10), in spite of the fact that the remains of reindeer included in the 7-5 sample are those with the highest structural density (Fig. 15), which exerts strong influences on the transportability of skeletal elements by fluvial processes (Voorhies, 1969). The negative
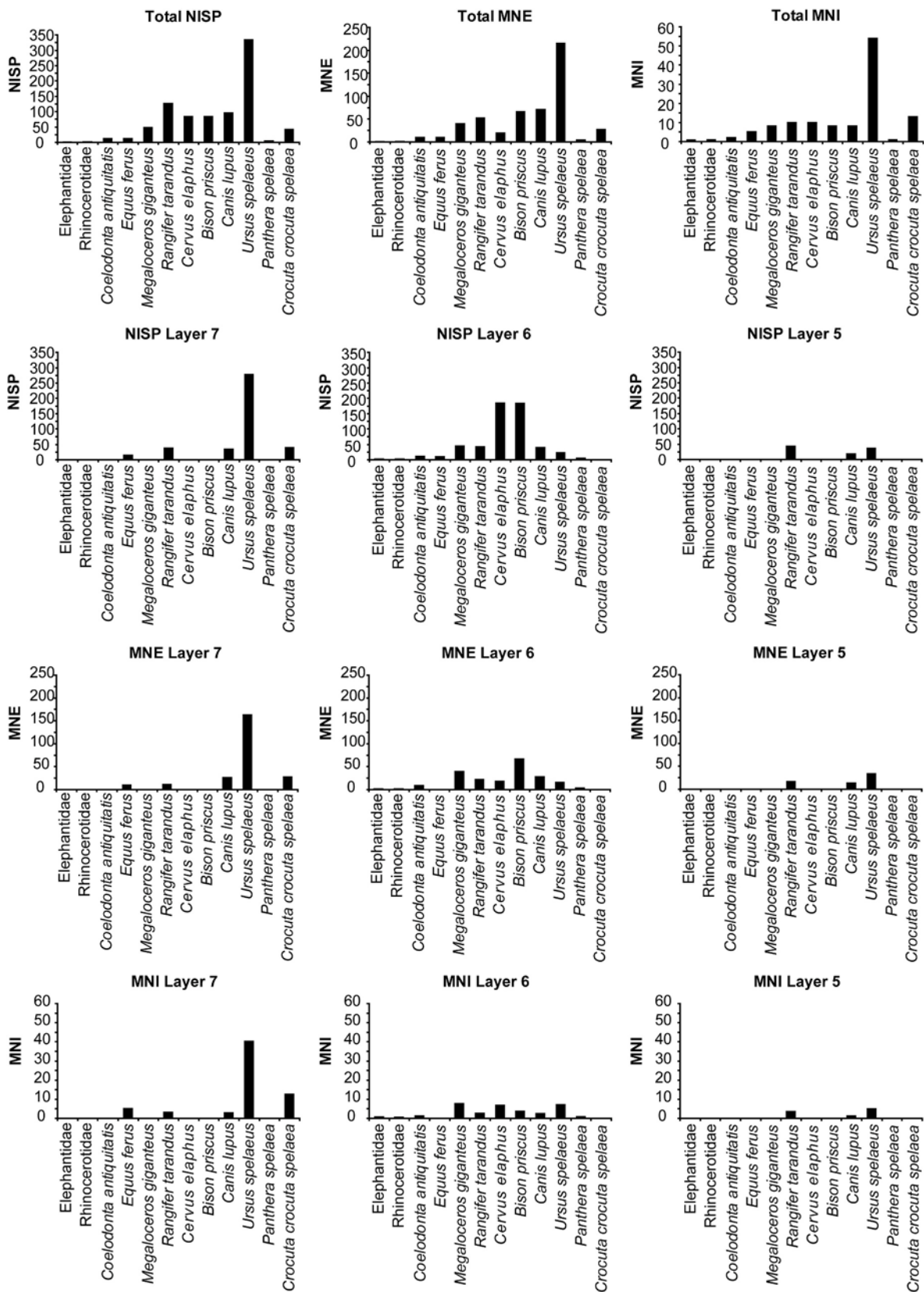
Fig. 4. Total NISP, MNE and MNI counts. The diagrams show particular abundances of *Ursus spelaeus*, *Crocuta crocuta spelaea*, *Rangifer tarandus*, *Bison priscus* and *Cervus elaphus*.

Table 3

Quantitative amounts of skeletal elements. NISP = Number of Identified Specimens; MNI = Minimum Number of Individuals; MNE = Minimum Number of Elements; MAU = Minimum Number of Animal Units; %MAU = Normed MAU values.

element	Elephantidae NISP	MNE	MAU	%MAU	Compete bones	NISP-complete bones	MNE-complete bones	MNI	Rhinocerotidae NISP	MNE	MAU	%MAU	Compete bones	NISP-complete bones	MNE-complete bones	MNI	Coelodonta antiquitatis NISP	MNE	MAU	%MAU	Compete bones	NISP-complete bones	MNE-complete bones	MNI
Antler fragments	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Shed antlers	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Skull	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1	–	–	–	3	1	1
Mandible	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Atlas	–	–	–	–	–	–	–	–	1	1	1	2,6667	–	1	1	1	1	1	1	2,6667	–	1	1	1
Axis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cervical vertebrae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thoracic vertebrae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lumbar vertebrae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Indet. vertebrae	1	1	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sacrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Caudal vertebrae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rib	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0,03	0,07	–	1	1	1
Scapula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0,5	1,33333	–	1	1	1
Humerus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0,5	1,33333	–	1	1	1
Radius/ulna	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	3	1,5	4	–	4	3	2
Carpal bones	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0,06	0,16	1	–	–	1
Metacarpal bones	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coxal bones	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Femur	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Patella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tibia	–	–	–	-	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0,5	1,33333	–	1	1	1
Astragalus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Calcaneum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Other tarsal bones	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Metatarsal bones	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I Phalanx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
II Phalanx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
III Phalanx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Anatomically indeterminate specimens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Total	1	1	–	–	–	–	1	1	1	1	–	–	–	1	1	1	14	10	–	–	–	12	9	2

element	Equus ferus NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI	Megaloceros giganteus NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI	Rangifer tarandus NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI
Antler fragments	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	–	–	11	–	–
Shed antlers	–	–	–	–	–	–	–	–	2	2	–	–	–	2	2	–	5	3	–	–	–	5	–	–
Skull	2	1	1	2,6667	–	2	1	1	14	8	8	21,333	–	14	8	8	27	6	6	16	–	27	6	6
Mandible	4	4	2	5333	–	4	4	4	4	4	2	5,3333	–	4	4	4	36	10	5	13,333	–	36	10	9
Atlas	–	–	–	–	–	–	–	–	1	1	1	2,6667	–	1	1	1	–	–	0	0	–	–	–	–
Axis	–	–	–	–	–	–	–	–	1	1	1	2,6667	–	1	1	1	–	–	0	0	–	–	–	–
Cervical vertebrae	–	–	–	–	–	–	–	–	2	2	0,4	1,0667	–	2	2	1	1	1	0,2	0,5333	–	1	1	1
Thoracic vertebrae	–	–	–	–	–	–	–	–	1	1	0,08	0,2133	–	1	1	1	–	–	–	–	–	–	–	–
Lumbar vertebrae	–	–	–	–	–	–	–	–	1	1	0,17	0,4444	–	1	1	1	–	–	–	–	–	–	–	–
Sacrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Caudal vertebrae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rib	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scapula	–	–	–	–	–	–	–	–	1	1	0,5	1,3333	-	1	1	1	–	–	–	–	–	–	–	–
Humerus	–	–	–	–	–	–	–	–	1	1	0,5	1,3333	–	1	1	1	–	–	–	–	–	–	–	–
Radius/ulna	–	–	–	–	–	–	–	–	2	2	1	2,6667	–	2	2	2	1	1	0,5	1,3333	–	1	1	1

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Table 3 (*continued*)

element	Elephantidae								Rhinocerotidae									Coelodonta antiquitatis							
	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete bones	MNE-complete bones	MNI	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete bones	MNE-complete bones	MNI	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete bones	MNE-complete bones	MNI
Carpal bones	–	–	–	–	–	–	–	–	5	5	0,31	0,8333	2	3	3	1	2	2	0,13	0,3333	1	1	1	1
Metacarpal bones	–	–	–	–	–	–	–	–	3	3	1,5	4	1	2	2	2	3	3	1,5	4	–	3	3	1
Coxal bones	–	–	–	–	–	–	–	–	2	2	1	2,6667	–	2	2	1	–	–	0	0	–	–	–	–
Femur	1	1	0,5	1,3333	–	1	1	1	–	–	0	0	–	–	–	–	2	1	0,5	1,3333	–	2	1	1
Patella	–	–	–	–	–	–	–	–	3	3	1,5	4	–	3	3	2	–	–	0	0	–	–	–	–
Tibia	1	1	0,5	1,3333	1	–	–	1	–	–	–	–	–	–	–	–	4	1	0,5	1,3333	–	4	1	1
Astragalus	3	3	1,5	4	3	–	–	2	–	–	–	–	–	–	–	–	2	2	1	2,6667	1	1	1	2
Calcaneum	–	–	–	–	–	–	–	–	1	1	0,5	1,3333	1	–	–	1	2	1	0,5	1,3333	–	2	1	1
Other tarsal bones	–	–	–	–	–	–	–	–	1	1	0,13	0,3333	1	–	–	1	3	2	0,25	0,6667	–	3	2	1
Metatarsal bones	–	–	–	–	–	–	–	–	3	3	1,5	4	–	3	3	1	2	2	1	2,6667	–	2	2	1
I Phalanx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	11	1,38	3,6667	2	9	9	2
II Phalanx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	7	0,88	2,3333	2	5	5	1
III Phalanx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	0,25	0,6667	–	2	2	1
Anatomically indeterminate specimens	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–
Total	12	10			4	7	6	5	48	42			5	43	37	8	125	55			6	115	46	10

element	Cervus elaphus								Bison priscus									Canis lupus							
	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI
Antler fragments	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Shed antlers	43	43	–	–	–	43	43	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Skull	21	7	7	18,667	–	21	7	6	11	4	4	10,667	–	11	4	4	23	6	6	16	–	23	6	6
Mandible	12	6	3	8	–	12	6	6	8	4	2	5,3333	–	8	4	4	18	13	6,5	17,333	–	18	13	9
Atlas	–	–	–	–	–	–	–	–	–	–	0	0	–	–	–	–	–	–	0	0	–	–	–	–
Axis	–	–	–	–	–	–	–	–	3	3	3	8	–	3	3	3	3	3	3	8	2	1	1	3
Cervical vertebrae	–	–	–	–	–	–	–	–	3	3	0,5	1,3333	–	3	3	3	–	–	–	–	–	–	–	–
Thoracic vertebrae	–	–	–	–	–	–	–	–	1	1	0,07	0,1905	–	1	1	1	1	1	0,003	0008	–	1	1	1
Lumbar vertebrae	–	–	–	–	–	–	–	–	1	1	0,2	0,5333	–	1	1	1	5	5	0,71	2	–	5	5	5
Sacrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	2,6667	–	1	1	1
Caudal vertebrae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	6	0,3	0,8	5	1	1	1
Rib	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0,04	0,1026	–	1	1	1
Scapula	–	–	–	–	–	–	–	–	2	2	1	2,6667	1	1	1	2	2	2	1	2,6667	–	2	2	1
Humerus	–	–	–	–	–	–	–	–	9	8	4	10,667	–	9	8	5	–	–	–	–	–	-	–	–
Radius/ulna	–	–	–	–	–	–	–	–	6	4	2	5,3333	1	5	3	4	5	2	1	2,6667	2	3	–	1
Carpal bones	–	–	–	–	–	–	–	–	3	3	0,19	0,5	3	–	–	1	1	1	0,14	0,381	1	–	–	1
Metacarpal bones	1	1	0,5	1,3333	–	1	1	1	6	5	2,5	6,6667	1	5	4	5	2	2	0,2	0,5333	2	–	–	1
Coxal bones	–	–	–	–	–	–	–	–	–	–	0	0	–	–	–	–	–	–	–	–	–	–	–	–
Femur	–	–	–	–	–	–	–	–	3	3	1,5	4	–	3	3	1	2	2	1	2,6667	–	2	2	1
Patella	–	–	–	–	–	–	–	–	–	–	0	0	–	–	–	–	1	1	0,5	1,3333	1	–	–	1
Tibia	1	1	0,5	1,3333	–	1	1	1	9	8	4	10,667	–	9	8	5	1	1	0,5	1,3333	–	1	1	1
Astragalus	2	1	0,5	1,3333	–	2	1	1	7	7	3,5	9,3333	6	1	1	4	1	1	0,5	1,3333	1	–	–	1
Calcaneum	2	1	0,5	1,3333	–	2	1	1	6	6	3	8	–	6	6	5	4	4	2	5,3333	4	–	–	3
Other tarsal bones	–	–	–	–	–	–	–	–	–	–	0	0	–	–	–	–	2	2	0,2	0,5333	2	–	–	2
Metatarsal bones	–	–	–	–	–	–	–	–	6	4	2	5,3333	–	6	4	2	3	3	0,3	0,8	2	1	1	1
I Phalanx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	4	0,2	0,5333	3	1	1	1
II Phalanx	–	2	0,25	0,6667	–	–	2	1	–	–	–	–	–	–	–	–	6	6	0,375	1	6	–	–	1
III Phalanx	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	4	0,2	0,5333	–	4	4	4
Anatomically indeterminate specimens	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	85	62			-	82	62	10	84	66	–	–	12	72	54	8	96	71			31	65	40	8

Table 3 (*continued*)

Top (continued) group headers: **Elephantidae** — element | NISP MNE MAU %MAU | Compete bones | NISP-complete bones | MNE-complete bones | MNI. **Rhinocerotidae** — NISP MNE MAU %MAU | Compete bones | NISP-complete bones | MNE-complete bones | MNI. **Coelodonta antiquitatis** — NISP MNE MAU %MAU | Compete bones | NISP-complete bones | MNE-complete bones | MNI.

element	Ursus spelaeus								Panthera spelaea								Crocuta crocuta spelaea							
	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI	NISP	MNE	MAU	%MAU	Compete bones	NISP-complete	MNE-complete	MNI
Antler fragments	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Shed antlers	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Skull	78	28	–	–	–	78	28	28	–	–	–	–	–	–	–	–	17	9	28	74,667	–	17	9	9
Mandible	138	75	–	–	–	138	75	55	–	–	–	–	–	–	–	–	19	14	37,5	100	–	19	14	10
Atlas	1	1	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	1	2,6667	–	–	–	–
Axis	1	1	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	1	2,6667	–	–	–	–
Cervical vertebrae	2	2	–	–	–	2	2	2	–	–	–	–	–	–	–	–	–	–	0,4	1,0667	–	–	–	–
Thoracic vertebrae	6	6	–	–	2	4	4	2	–	–	–	–	–	–	–	–	–	–	0,46	1,2267	–	–	–	–
Lumbar vertebrae	2	2	–	–	–	2	2	1	–	–	–	–	–	–	–	–	–	–	0,33	0,88	–	–	–	–
Sacrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	–	–	–	–
Caudal vertebrae	1	1	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	0,13	0,3467	–	–	–	–
Rib	7	3	–	–	–	7	3	2	–	–	–	–	–	–	–	–	–	–	0,12	0,32	–	–	–	–
Scapula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	–	–	–	–
Humerus	1	1	–	–	–	1	1	1	–	–	–	–	–	–	–	–	1	1	0,5	1,3333	–	1	1	1
Radius/ulna	2	2	–	–	–	2	2	2	–	–	–	–	–	–	–	–	–	–	1	2,6667	–	–	–	–
Carpal bones	11	11	–	–	9	2	2	3	–	–	–	–	–	–	–	–	1	1	0,79	2,1067	1	–	–	1
Metacarpal bones	6	6	–	–	6	–	–	2	2	2	–	–	2	–	–	1	–	–	0,6	1,6	–	–	–	–
Coxal bones	-	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	–	–	–	–
Femur	5	5	–	–	–	5	5	3	–	–	–	–	–	–	–	–	–	–	2,5	6,6667	–	–	–	–
Patella	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	–	–	–	–
Tibia	2	2	–	–	1	1	1	2	–	–	–	–	–	–	–	–	–	–	1	2,6667	–	–	–	–
Astragalus	3	3	–	–	3	–	–	3	–	–	–	–	–	–	–	–	–	–	1,5	4	–	–	–	–
Calcaneum	1	1	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	0,5	1333	–	–	–	–
Other tarsal bones	6	6	–	–	6	–	–	2	–	–	–	–	–	–	–	–	–	–	0,6	1,6	–	–	–	–
Metatarsal bones	19	19	–	–	11	8	8	7	1	1	–	–	–	1	1	1	–	–	1,9	5,0667	–	–	–	–
I Phalanx	26	26	–	–	15	11	11	3	–	–	–	–	–	–	–	–	1	1	1,3	3,4667	1	–	–	1
II Phalanx	9	9	–	–	9	–	–	1	–	–	–	–	–	–	–	–	1	1	0,56	1,4933	1	–	–	1
III Phalanx	5	5	–	–	5	–	–	1	1	1	–	–	–	1	1	1	–	–	0,25	0,6667	–	–	–	–
Anatomically indeterminate specimens	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Total	334	215	–	–	69	263	146	54	4	4	–	–	2	2	2	1	42	27	–	–	3	37	24	13
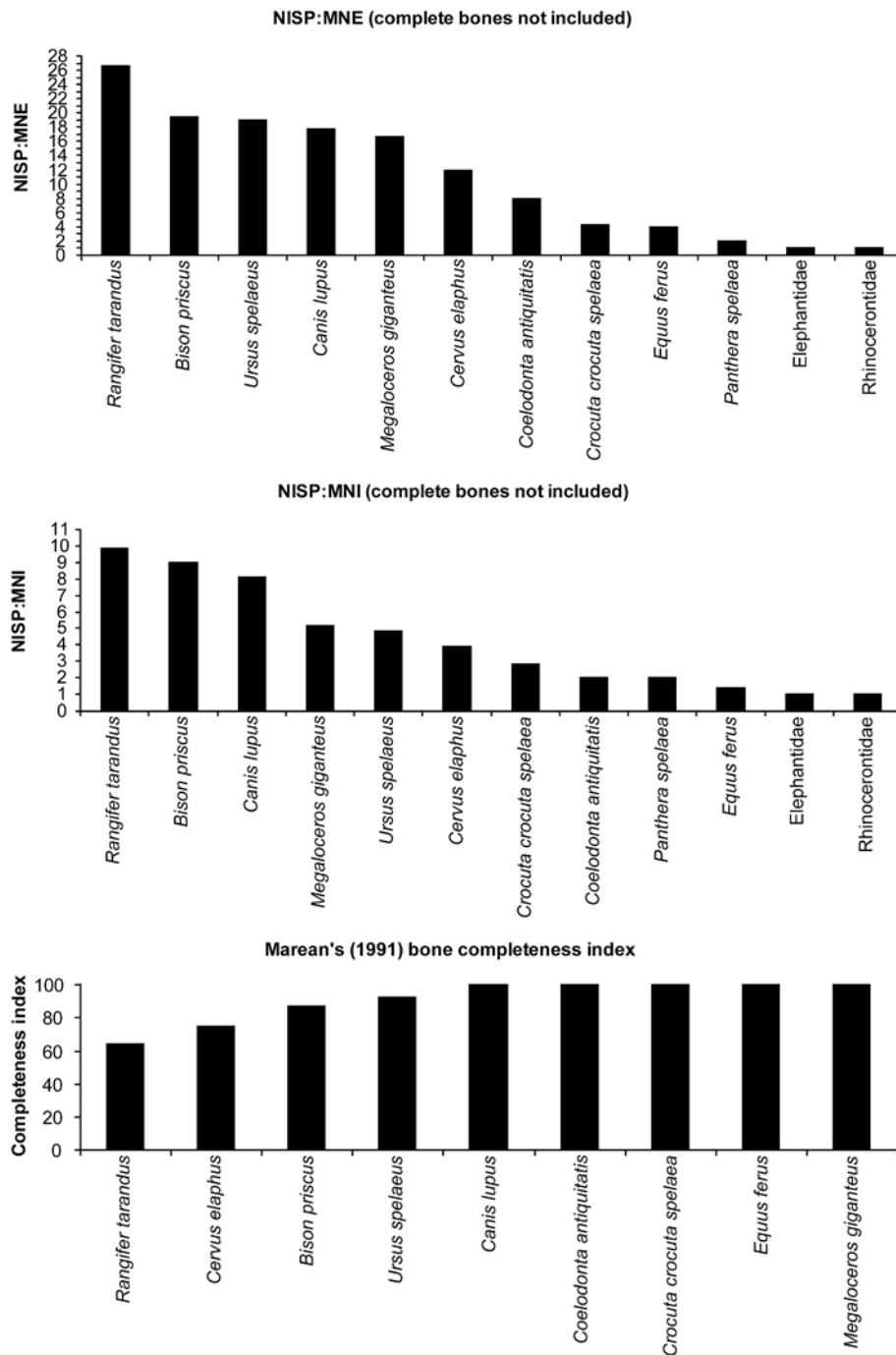
Fig. 5. NISP:MNE ratio, NISP:MNI ratio and Marean's (1991) bone completeness index; taxonomic order based on decreasing index values. The diagrams show that the remains of *Rangifer tarandus*, *Bison priscus*, *Ursus spelaeus*, *Canis lupus* and *Megaloceros giganteus* are particularly fragmented.
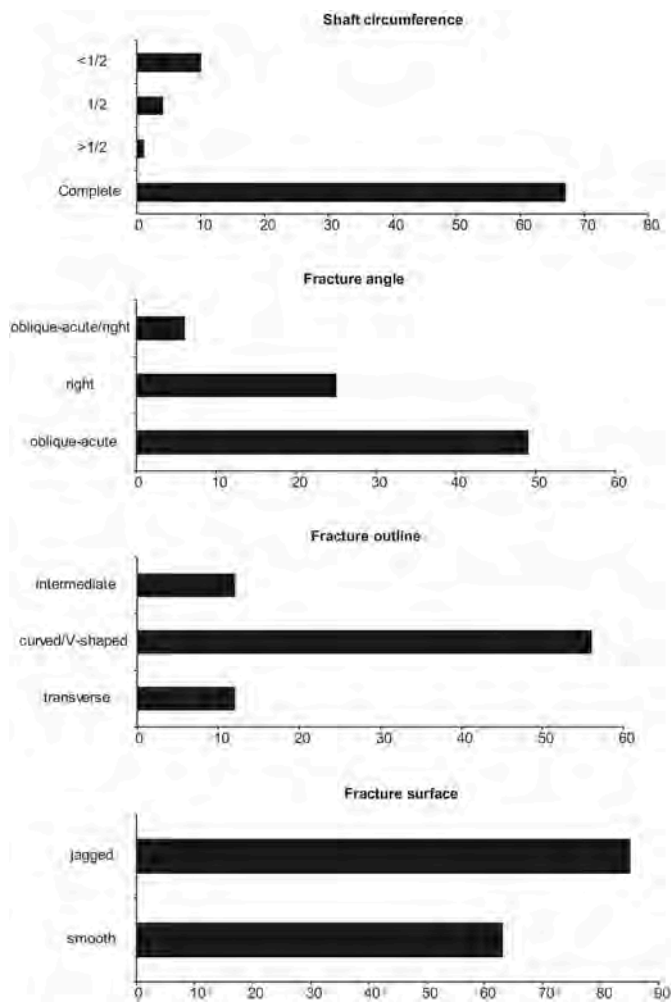
Fig. 6. Relative frequencies of the fracture angles, fracture outlines and fracture edges, and completeness of the limb bone shaft circumferences. Approximately equivalent numbers of limb bones were broken in both dry and brittle state and in green bone state.

correlation obtained for *Rangifer* therefore shows that the SWI values estimated for topi antelopes cannot be used for testing the susceptibility of reindeer bones to fluvial transport.

4.4. Bone modification

Breakage apart, Biśnik Cave's 7–5 specimens exhibit numerous cortical modifications (Fig. 16, Fig. 9, Fig. 17, Table 4). The most frequent non-carnivore- and non-hominin-derived alteration is corrosion; the highest incidence was found in the bones of *U. spelaeus* and *C. lupus*. In contrast, teeth appear unaffected by this phenomenon. The second most frequent abiotic modification is abrasion/polishing, which is especially observed on the bones of *U. spelaeus* and of the cervids. Trampling evidence was primarily found on remains of *B. priscus* and *U. spelaeus*, less frequently on those of cervids and *C. c. spelaea*, and rarely on those of the other taxa. Plant root/fungal/bacterial tunneling is not so infrequent to find, primarily on bones of *B. priscus*, *U. spelaeus*, and secondarily on those of *M. giganteus* and *C. lupus*. Only 46 specimens show evidence of weathering, but in most cases this alteration consists of fissures, which indicate very modest exposure (weathering stages 1 and 1–2).

Based on Pobiner et al.'s (2020) bone damage and destruction counts, the animals most targeted by carnivores are *Megaloceros giganteus* and *Bison priscus*. More specifically, counts show 61 specimens in
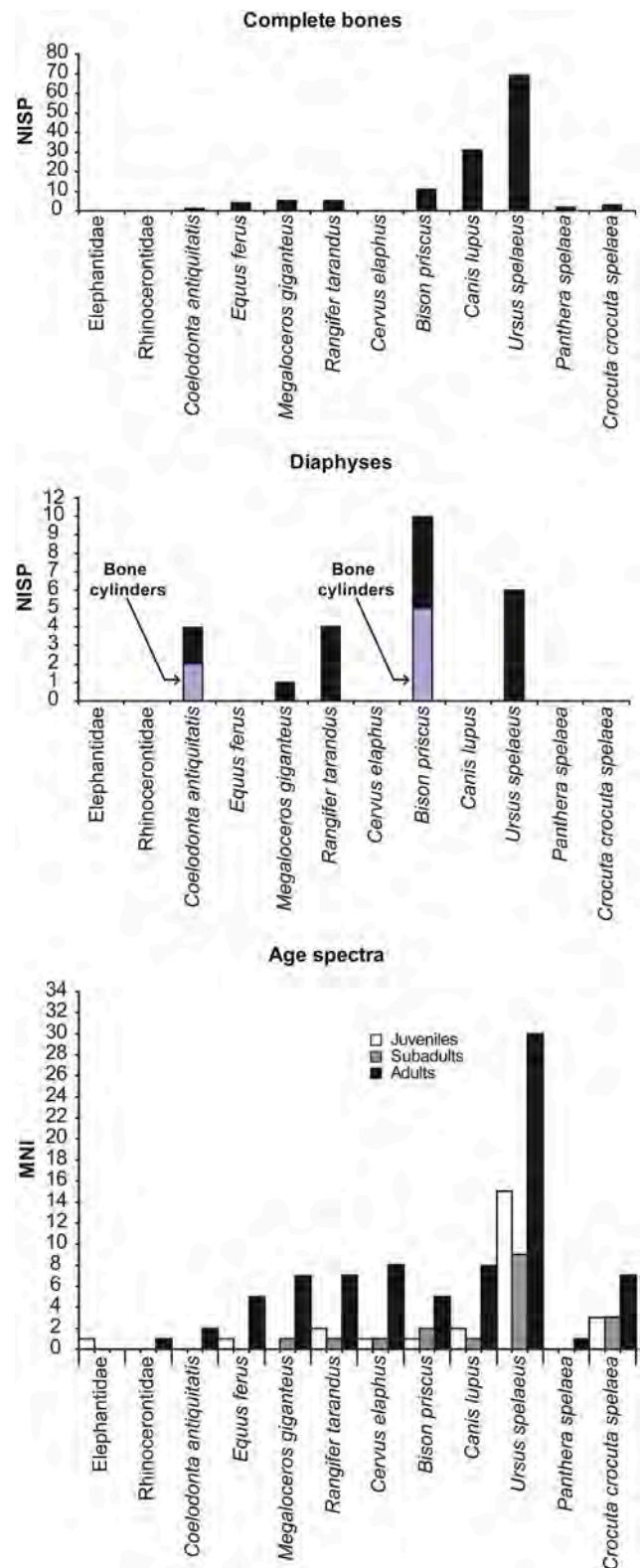
Fig. 7. Number of complete bones, and of diaphyses per taxon, expressed in NISP counts, and overall age spectra per taxon, expressed in MNI counts. *Ursus spelaeus* and *Canis lupus* include the relatively highest amounts of complete bones. Limb bones including only shaft portions are most numerous in *Bison priscus* and *Ursus spelaeus*. Specimens in the form of "bone cylinders" belong to *Bison priscus* and *Coelodonta antiquitatis*. The age spectra diagram shows a typical "U-shaped", attritional death pattern in the case of *Ursus spelaeus*.
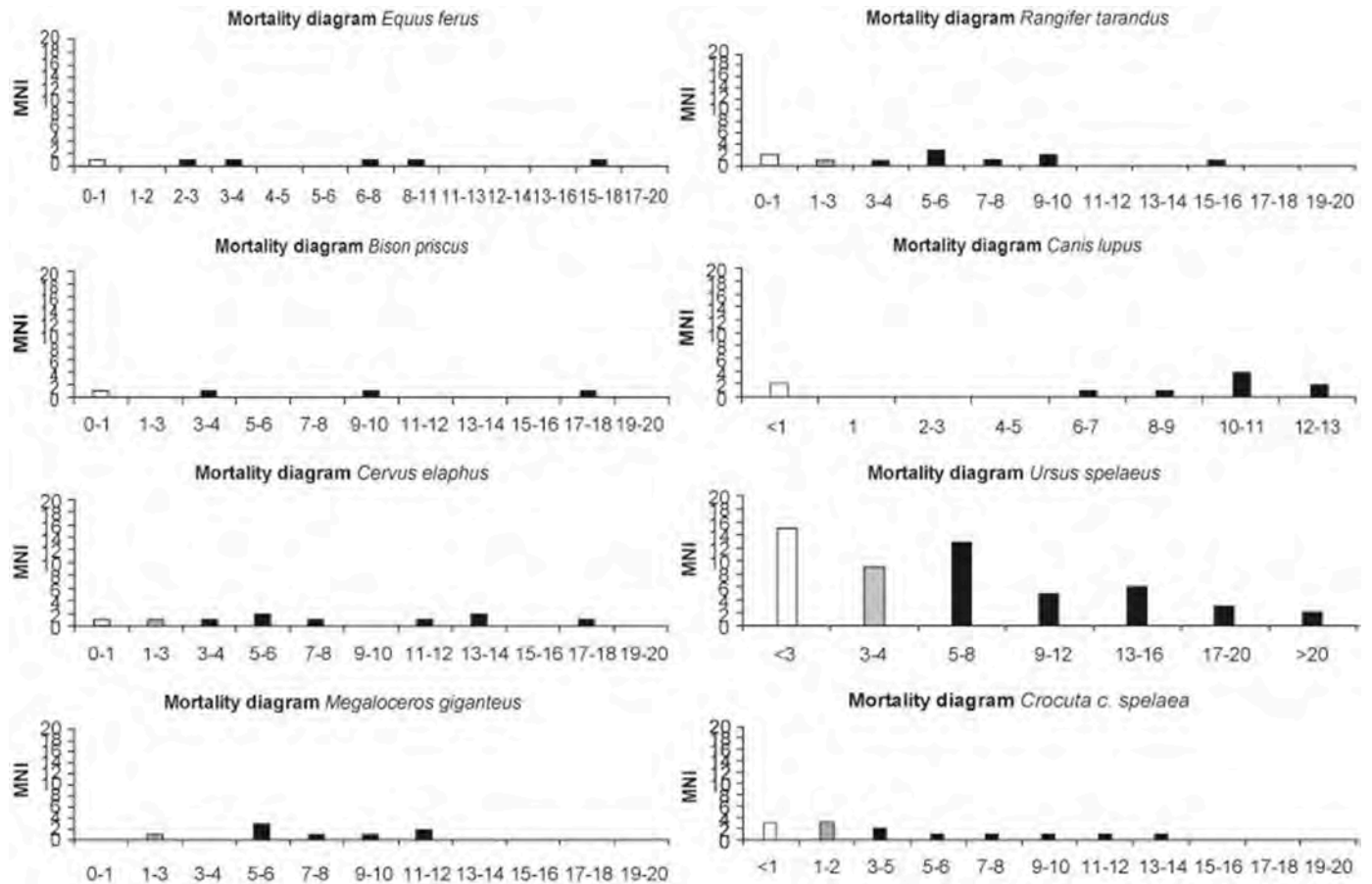
Fig. 8. Mortality diagrams of *Equus ferus*, *Bison priscus*, *Cervus elaphus*, *Megaloceros giganteus*, *Rangifer tarandus*, *Canis lupus*, *Ursus spelaeus* and *Corcuta crocuta spelaea*, based on degree of long bone epiphyseal fusion, degree of ossification, antler development and tooth eruption and wear. The diagrams exhibit relatively higher amounts of adult/senile individuals than of juveniles and sub-adults in all the taxa but *Ursus spelaeus*, in which juveniles and sub-adults are much better represented.

Fig. 9. Examples of taphonomic modifications observed on the Biśnik Cave bones. A) Inv. nr. ? 1606, proximal part of left radius of *Coelodonta antiquitatis*, palmar view. The diaphysis shows a spiral tension failure (green- or fresh-bone fracture), and cortically trampling scratches and plant root/fungal/bacterial tunneling (arrow). The specimen exhibits black manganese coatings. B) Inv. nr. ? 1606, proximal part of left radius of *Coelodonta antiquitatis*, dorsal view. Detail of fresh-bone fracture (arrow) at the distal end of the specimen. C) Inv. nr. 1697, diaphysis of left femur of *Bison priscus*, medial view. Both epiphyses missing (bone cylinder), fresh bone fractures (arrow) likely produced by trampling. Cortically, the specimen shows trampling scratches and many root/fungal/bacterial tunnelings on the cranial face, but no bites nor gnawing marks. D) Inv. nr. 1697, diaphysis of left femur of *Bison priscus*, medial view. Detail of fresh-bone fracture (upper arrow) at the proximal end of the specimen and of trampling scratches (lower arrows). Note the black manganese coatings, especially on the inner surfaces of the remain. E) Inv. nr. 1697, diaphysis of left femur of *Bison priscus*, proximal view. F) Inv. nr. B 182 96 8?, proximo-dorsal portion of left metatarsal bone of *Bison priscus*, dorsal view. G) Inv. nr. B 182 96 8?, proximo-dorsal portion of left metatarsal bone of *Bison priscus*, plantar view. The specimen exhibits various trampling scratches and root/fungal/bacterial tunnelings extended over the fractures, which were produced when the bone was still in fresh state (arrows). The specimen is extensively coated with manganese. Scale bars 5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

damage level 2, 33 in damage level 3 and 6 in damage level 4. The less damaged are remains of medium to large sized animals (*Rangifer tarandus*, *Equus ferus*, *Cervus elaphus*, *Ursus spelaeus*, *Megaloceros giganteus*), those in damage level 3 are practically all medium to very large sized animals (*C. elaphus*, *M. giganteus*, *Bison priscus*, *Coelodonta antiquitatis*), with the only exception of a humerus of *Crocuta crocuta spelaea*, and the most ravaged by carnivores are remains of large sized animals (*M. giganteus*, *B. priscus*). Carnivore-ravaging evidence largely consists of bites and gnawing marks (Fig. 9, Fig. 17); gastric corrosion is rarer
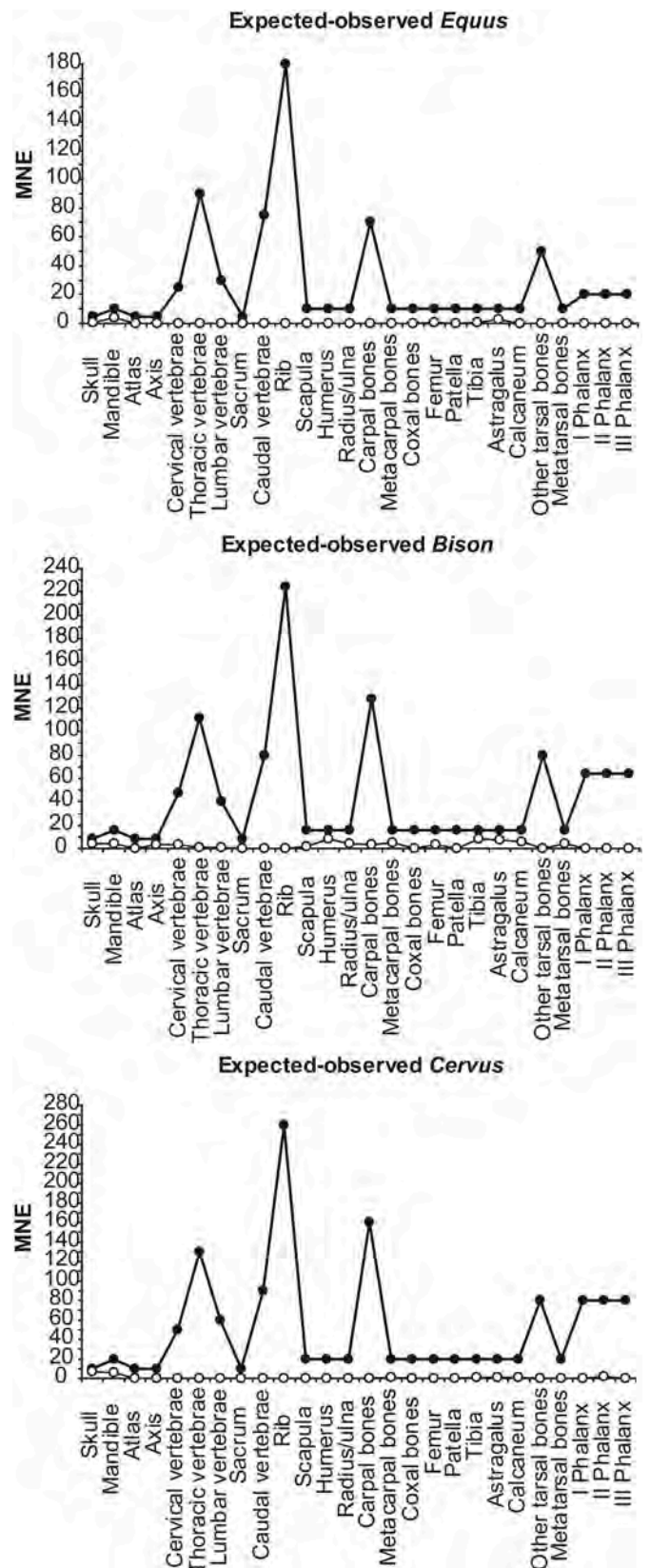
Fig. 10. Observed versus MNI-based expected amounts of bones in *Equus ferus*, *Bison priscus*, and *Cervus elaphus*, expressed in MNE counts. There is a marked under-representation of axial bones, basipodial bones, and phalanges.
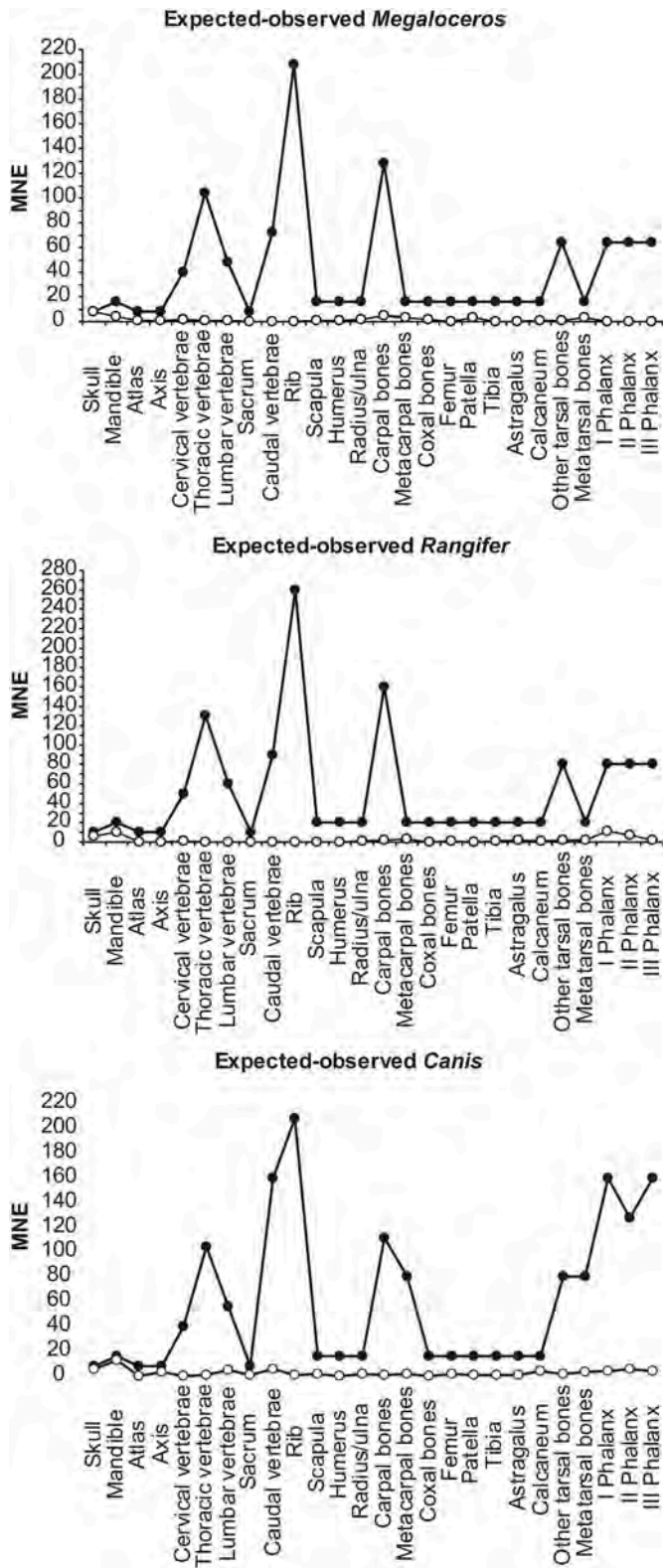
Fig. 11. Observed versus MNI-based expected amounts of bones in *Megaloceros giganteus*, *Rangifer tarandus*, and *Canis lupus*, expressed in MNE counts. There is a marked under-representation of axial bones, basipodial bones, and phalanges in all the taxa.
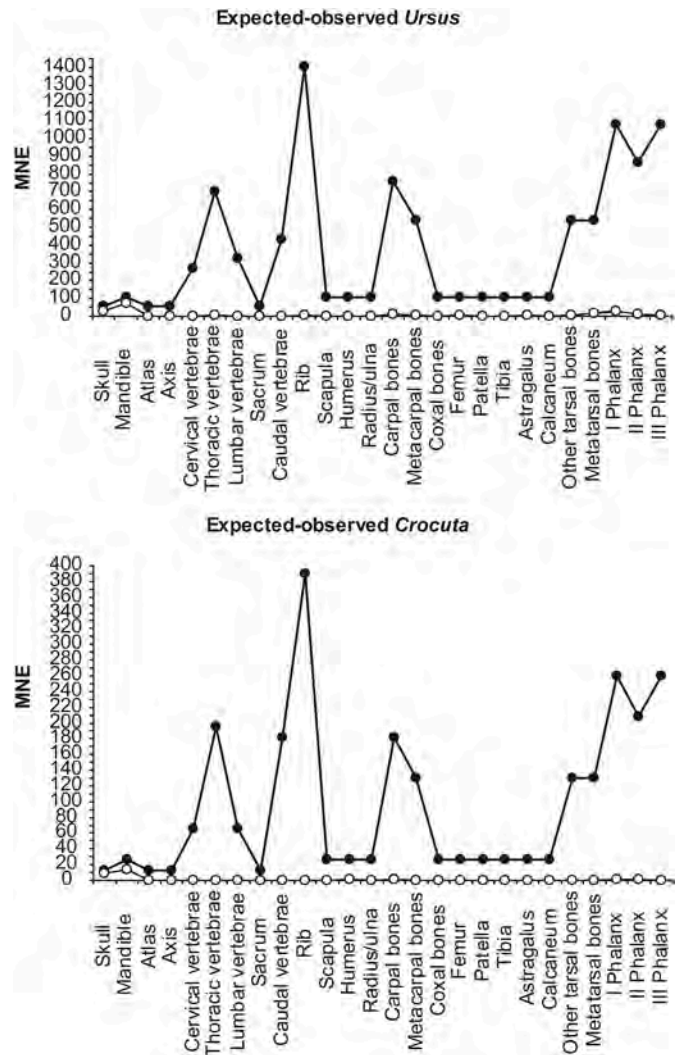
Fig. 12. Observed versus MNI-based expected amounts of bones in *Ursus spelaeus* and *Crocuta crocuta spealea*, expressed in MNE counts. There is a marked under-representation of axial bones, basipodial bones, and phalanges.
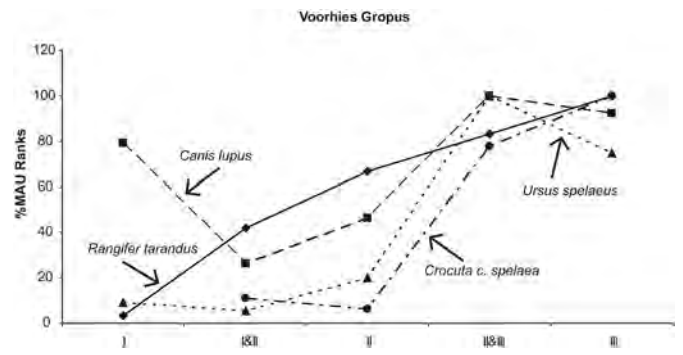
Fig. 13. Voorhies' Groups, expressed in %MAU counts. The diagram shows that in the cases of all four the examined species, i.e., *Rangifer tarandus*, *Canis lupus*, *Ursus spelaeus* and *Crocuta crocuta spealea* there are proportionally far higher amounts of Group II and III and III bones. *Rangifer tarandus* also shows relatively high numbers of Group I and II and II bones, and *Canis lupus* of Group I and II bones.
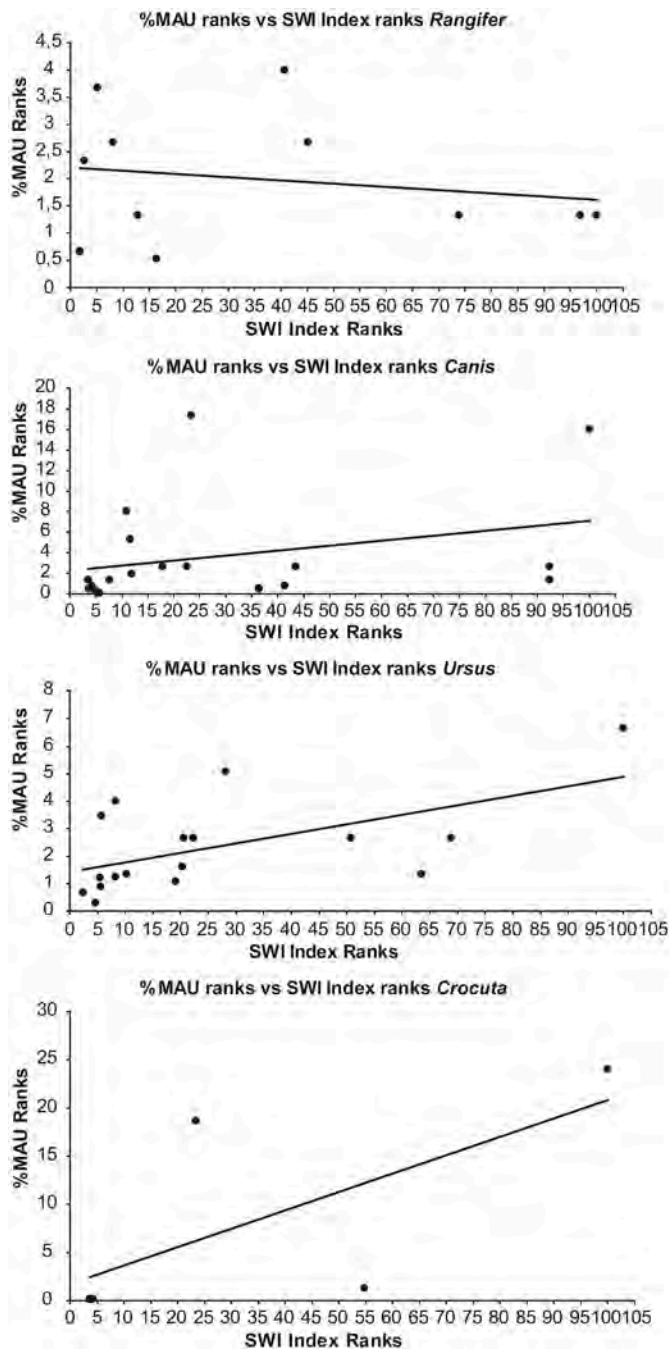
Fig. 14. % MAU ranks vs SWI index ranks in *Rangifer tarandus*, *Canis lupus*, *Ursus spelaeus* and *Corcuta crocuta spelaea*. All the diagrams but that for *Rangifer tarandus* show highly significant, positive correlations.

(Fig. 16). Many specimens are punctured by single tooth-cusp pits and their surfaces are grooved by numerous tooth scores. Bone ends and antler parts are often partially or entirely removed, and the diaphyses show jagged/festooned fracture edges, which may sometimes be rounded by insisted gnawing. Deep, about 3–5 mm wide and 3–5 mm deep, cone-shaped and round-bottomed furrows and impressions are frequently carved in the inner cancellous of epiphyses and antlers. Long bone diaphyses are often scored transversely to the long axis. Alongside this kind of damage, isolated or sets of single tooth punctures, furrows and impressions can be observed through cortical compact bone into the trabecular tissue and the cancellous bone of antlers. Tooth scratches over 3 cm long, 1 mm deep and up to 2–3 mm wide can be observed running transversely or diagonally to the long axis of long bone shafts or carved in the trabecular bone of limb bone ends as well as in exposed trabecular bone of chopped off antler ends. More rarely, narrower and shallower tooth scores can be observed at right angles or diagonal to the long axis of limb bone elements or scored through exposed cancellous epiphyseal bone of gouged bone ends.

A total of 70 antlers was retrieved from layers 7–5; 51 of them are naturally shed antlers: 42 are of *C. elaphus*, 7 of *R. tarandus* and 2 of *Megaloceros giganteus*. With the only exception a fragmental left femur of *R. tarandus*, marks of possible hominin modification were observed exclusively on antler fragments, of both *C. elaphus* and *R. tarandus* (Fig. 16), and only one of them, W/1606 of *C. elaphus*, is unshed. These purportedly humanly modified antlers show a common processing pattern: almost the entire beam is removed, together with both basal tines and crown above the bez tine (Fig. 16). The margins of the chopped beam and tine stumps are either well rounded from carnivore chewing abrasion, or polished from corrosion, or both. Other modifications observed on some of the shed antlers from layers 7–5 include the presence of pits, scores and grooves in the centre of the convex surface under the burr (Fig. 17) and the partial or complete removal of the inner trabecular bone from 11 specimens.

4.5. Antler analysis

Despite many specimens are covered by a consolidant that prevents the analysis of their surface, several shed antlers from layer 7 underwent substantial post-depositional alteration. The cortical bone of these specimens is weathered. Some of them exhibit both abiotic, mechanical and post-depositional damage, and evidence of predator or scavenger disturbance. Only three antlers of *Cervus elaphus* (no. W/1689, W/1717 and W/1639) exhibit possible traces of anthropogenic processing. Another one, of *Rangifer tarandus*, (W/825) shows signs of battering.

4.5.1. W/1689 (layer 7, niche inside the main chamber, group E, middle Palaeolithic)

The antler cortical bone is completely removed; the surface appears smooth and matted. Edges and protruding parts of the antler are rounded. Deep bite marks are apparent at the ends of the tine stumps.

An individual, possibly tool-generated incision is present on the end of the brow tine stump (Fig. 18A). This mark is perhaps the result of a
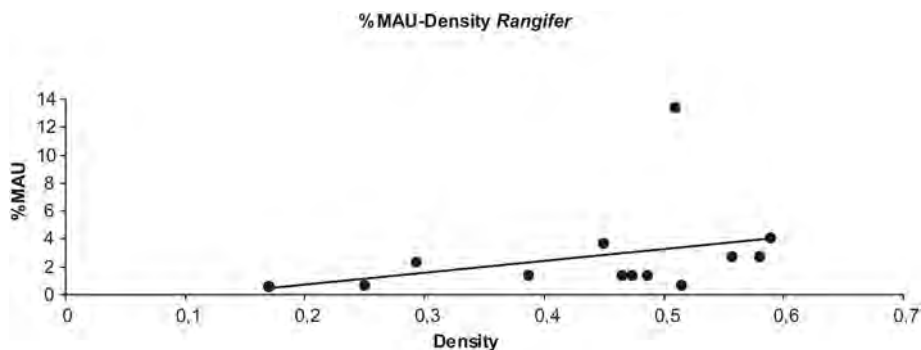
Fig. 15. % MAU vs Bone Density in *Rangifer tarandus*. The diagrams show highly significant, positive correlation.
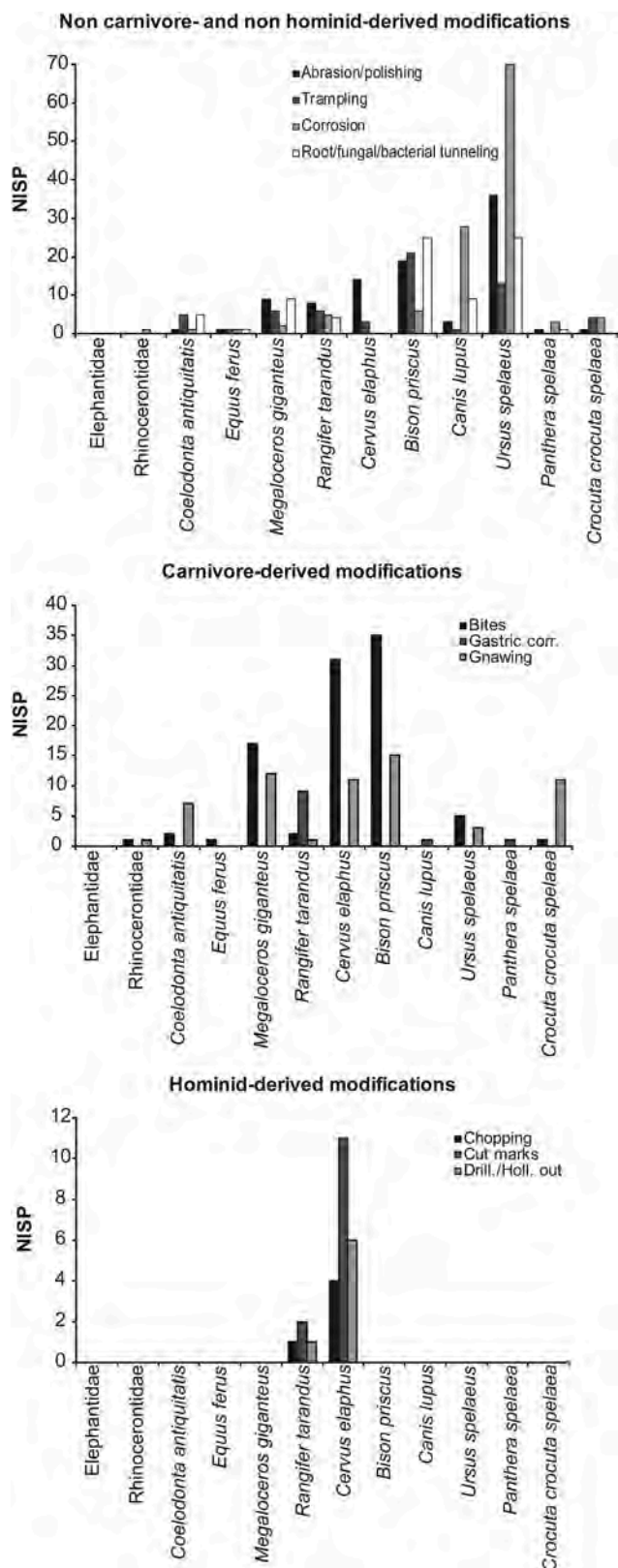
Fig. 16. Incidence of bone surface modification. Corrosion is the dominant abiotic alteration, and the second most frequent is abrasion/polishing. Carnivore-derived damage, largely bites and gnawing marks, is prevalently observed on remains of cervids and *B. priscus*. Hominin modification was only observed on antler fragments.

percussion on the antler surface. The mark has clear-cut borders and is located in an area coloured differently from the rest of the antler; unfortunately, it is coated by a consolidant which complicates the interpretation of its origin.

4.5.2. W/1717 (layer 7, niche inside the main chamber, group E, middle Palaeolithic)

The cortical bone of the specimen is totally removed. Edges and protruding parts of the antler are rounded. The ends of the tine stumps exhibit deep bite marks.

Three grooves, V-shaped in transverse cross-section, are visible near the end of the brow tine stump (Fig. 18B). These scars likely mark the impacts of a tool. However, possible internal features of the traces, potentially diagnostic of intentional modification, have been obliterated by the corrosion damage visible on the antler surface.

4.5.3. W/1639 (layer 7, niche inside the main chamber, group E, middle Palaeolithic)

Also in this case, the outer bone is entirely removed, the surface appears smooth and matted, and the edges and protruding parts of the antler are rounded. Deep bite marks are present at the ends of the tine stumps. A wide, deep and relatively long scar, or notch, V-shaped in transverse cross-section, is present on the edge of the brow tine stump (Fig. 18C). The trace is deeper in its central part than at both ends. Like in W-1717, the outer corrosion damage of the antler and the absence of internal features of the scar makes it impossible to ascertain if the mark is actually an intentional modification.

4.5.4. W/825 (layer 7, main chamber, aggregation of bones and flint products, group E, middle Palaeolithic)

Large, unwanted parts of the antler were removed. The surface of the preserved base of the bez tine exhibits striations characteristic of grinding (Fig. 19A). The traces appear as a set of relatively short, grouped scratches, oriented parallel to one another. Nearly the entire surface of the antler was roughly scraped (Fig. 19B). The grooves are invasive, largely oriented parallel to the long axis of the antler beam. Within these grooves and along their lengths are closely spaced microstriations (Fig. 19C). Clear use-wear marks are present on the base of the burr, as well as under it (Fig. 19D). Some damages are V-shaped in transverse cross-section and are well delineated (Fig. 19F). Under the burr, there are numerous overlapping and inter-cutting percussion pits, cuts and scores (Fig. 19E). In some areas pits of various depths are visible, associated with numerous striae and notches (Fig. 19G).

5. Discussion

The result of the taphonomic analysis indicates that Biśnik Cave's 7–5 fossil assemblage had a long and complex taphonomic history. It is a time-averaged palimpsest of remains from many successive generations of animals and hominins that frequented the cave, but also of episodic abiotic events.

5.1. Zooarchaeological and taphonomic remarks

Overall, the dominance and wide range of ontogenetic ages represented in the 7–5 fossil record indicate that Biśnik Cave was a favourite shelter for hibernating cave bears over a long period of time (Stefaniak and Marciszak, 2009; Marciszak et al., 2011a; Krajcarz et al., 2014b), but it also served as hyaena lair early in the history of the studied section. Hibernation-related deaths of bears arising from nonviolent causes, i.e., starvation, disease, as well as senescence, are typically dominated by juveniles, subadults and very old adults (Stiner, 1998). The peaks of juvenile and subadult cave bears from Biśnik Cave (Fig. 8; Table 1), as well as the low carnivore-derived damage on the cave bear bones (Fig. 16), perhaps inflicted on already dry bones lying exposed on the cave floor, indicate the presence of remains of individuals died largely

Fig. 17. Examples of taphonomic modifications observed on the Biśnik Cave bones. A) Inv. nr. 1705, atlas of *Coelodonta antiquitatis*, cranial view. The specimen has black manganese coatings. B) Inv. nr. 1705, atlas of *Coelodonta antiquitatis*, dorsal view. Note the crenulated margins of the wings (arrows), due to carnivore gnawing. C) Inv. nr. 1705, atlas of *Coelodonta antiquitatis*, caudal view. Wings (upper arrows) and ventral tubercle (lower arrow) have been deeply furrowed and scooped out by carnivores. D) Inv. nr. 1705, atlas of *Coelodonta antiquitatis*, ventral view. Arrows indicate the crenulations made by carnivore gnawing. E) Inv. nr. 1683, diaphysis of left tibia of *Coelodonta antiquitatis*, plantar view. Note the deep furrows caused by carnivore gnawing (upper arrow) and the plant root/fungal/bacterial tunnelings (lower arrow). F) Inv. nr. 1683, diaphysis of left tibia of *Coelodonta antiquitatis*, dorso-medial view. On this face the specimen exhibits parallel and subparallel, non-sinuous, grazes (sensu Courtenay et al., 2020) made by trampling (arrows). G) Inv. nr. 1683, diaphysis of left tibia of *Coelodonta antiquitatis*, dorso-proximal view. The specimen displays deep internal corrosion. H–I) Inv. nr. 1489, right hemi-mandible of *Megaloceros giganteus*, medial and lateral view, respectively. The specimen has extensive black manganese coatings and its angle is scooped out by carnivores (arrows). J) Inv. nr. 1757, distal half of left humerus of *Bison priscus*, caudal view. Epitrochlea (lower arrow) and epicondyle gnawed and scooped out by carnivores. The diaphysis displays a green bone fracture at the proximal end and cortically plant root/fungal/bacterial tunnelings (two upper arrows). K) Inv. nr. 1757, distal half of left humerus of *Bison priscus*, lateral view. Note the epicondyle scooped out by carnivores and the plant root/fungal/bacterial tunnelings (arrow). L) Inv. nr. 1757, distal half of left humerus of *Bison priscus*, distal view. Epitrochlea and epicondyle gnawed and scooped out by carnivores (arrows). Scale bars 5 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4
Incidence of bone modifications.

Taxa	Non-carnivore- and non-hominin-derived alterations																			
	Abras/polish.				Trampling				Corrosion				Root etch.				Bites		
	Observations	% to Total[a]	% to Total[b]	% to Total[c]	Observations	% to Total[a]	% to Total[b]	% to Total[c]	Observations	% to Total[a]	% to Total[b]	% to Total[c]	Observations	% to Total[a]	% to Total[b]	% to Total[c]	Observations	% to Total[a]	% to Total[b]
Elephantidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhinocerotidae	–	–	–	–	–	–	–	–	1	0,8	33,3	0,2	–	–	–	–	1	1,1	33,3
C. antiquitatis	1	1,1	4,8	0,2	5	8,3	23,8	0,9	1	0,8	4,7	0,2	5	6,3	23,8	0,9	2	2,1	9,5
E. ferus	1	1,1	20	0,2	1	1,7	20	0,2	1	0,8	20	0,2	1	1,3	20	0,2	1	1,1	20
M. giganteus	9	9,7	16,4	1,7	6	10	10,9	1,1	2	1,6	3,6	0,4	9	11,4	16,4	1,7	17	17,9	30,9
R. tarandus	8	8,6	20,5	1,5	6	10	15,4	1,1	5	4,1	12,8	0,9	4	5,1	10,3	0,7	2	2,1	5,1
C. elaphus	14	15,1	17,5	2,6	3	5	3,8	0,6	–	–	–	–	–	–	–	–	31	32,6	38,8
B. priscus	19	20,4	15,7	3,5	21	35	17,4	3,9	6	4,9	4,9	1,1	25	31,6	20,7	4,6	35	36,8	28,9
C. lupus	3	3,2	7,1	0,6	1	1,7	2,4	0,2	28	23,1	66,7	5,1	9	11,4	21,4	1,7	–	–	–
U. spelaeus	36	38,7	23,7	6,6	13	21,7	8,6	2,4	70	57,8	46	12,8	25	31,6	16,4	4,6	5	5,3	3,3
P. spelaea	1	1,1	16,7	0,2	–	–	–	–	3	2,4	50	0,6	1	1,3	16,7	0,2	–	–	–
C. c. spelaea	1	1,1	4,8	0,2	4	6,7	19	0,7	4	3,2	19	0,7	–	–	–	–	1	1,1	4,8
Totals[a]	93				60				121				79				95		

from non-violent, hibernation-related mortality.

Bears are highly vulnerable during winter retreats. This makes them very aware of the presence of other predators, bears included, or even of humans, and careful in keeping secret their hibernation lairs, to minimise the risk of intrusions. If they sense the presence of intruders in a potential lair, they are capable to avoid the place for very long periods of time, even generations. For this reason, hibernating bears are typically secretive and solitary (Hissa, 1997; Hissa et al., 1994; Mace and Waller, 1997; Roth et al., 1996). Lairs are thus generally occupied by a single individual, or a mother with cub(s), at the time. The high number of individuals of *U. spelaeus* from Biśnik Cave's layer 7–5 indicates a recurrent use of the cave by bears, and an attritional accumulation of their carcasses, over a long time period. More specifically, the quantitative counts performed for this study reveal that the cave was primarily used by cave bears at the time of deposition of layer 7, and sporadically thereafter (Fig. 4). Because of the bears' watchful behaviour, the competition with hyaenas and wolves in the use of the cave means that layer 7 is time-averaged, possibly more than the other two following layers. Mortality rate of cave bear cubs was between 46.2 and 78.9% (Robu, 2016; Veitschegger et al., 2019), which means, on average, roughly 63%. Curiously, this value is equivalent to the mean of the overall mortality rates measured over the entire lifespans of modern bears (Bunnell and Tait, 1980). With this rate of mortality and an average longevity around 20 years, assuming sequential, yearly deaths of one individual after the other, which, in fact, is unlikely, the 15 bear cubs from layer 7–5 would indicate an overall time span of at least 24 years, the 9 subadults 15 years and the 30 adults 48 years, for a total of up to 87 years. The unnatural association of the cave bear remains with those of other predators, as well as with hominin stone tools, but also the discontinuous, episodic accumulation of layer 7–5 is strong evidence that the assemblage is a long time-averaged palimpsest of diachronous events of exclusive occupation by bears, hyaenas, canids and hominins, that often appear misleadingly synchronous. In agreement with this, the breakage in dry state of their bones indicates that bears and canids occupied the cave at different times from each other and from the other species of the assemblage, whereas from their prevalently fresh state of breakage the remains of *Bison* accumulated in the cave together with those of the carnivores that presumably fed on them. All this significantly increases the length of time for accumulating the fossil assemblage by many orders of magnitude.

The high number of ruminant specimens displaying evidence of carnivore damage (Fig. 16; Fig. 17) are likely the residues of carcass parts introduced in Biśnik Cave by predators, perhaps primarily hyaenas and wolves. The involvement of both these predators is confirmed by the shapes and sizes of the carnivore scats found associated with level 7–5's bones (Fig. 20).

The numerous ruminant remains therefore likely represent, in accordance with Simms' (1994) classification, biotic allochthonous components of the assemblage. Added to them are also the gnawed long bone cylinders from layer 7, as well as the few carnivore-ravaged rhinocerotid and equid specimens from layer 6 (Fig. 7). The remains of both prey and predators are therefore assumed to have accumulated together, at a different time from those of the cave bears, for the reasons given above.

There are also rarer predator-damaged carnivore bones (Fig. 16). Although scarce, these remains can be related to deaths that occurred from violent predation, and/or to scavenging of already dead carcasses or carcass parts, both inside and outside the cave. Possibilities range widely, from violent deaths during hibernation (in the case of bears), to cannibalism.

While resting on the cave floor, Biśnik Cave's 7-5 bones have been exposed for some time to humid, oxidizing, alkaline conditions; but they have also been subjected to mechanical alterations. Overall, the limited trampling damage observed on some specimens indicates that there were low volumes of traffic inside the cave, at least during the deposition of the 7-5 sediments. Nonetheless, with regards to this, the breakage in dry state of the bones of *Ursus* and *Canis* indicates that the skeletal parts of these animals had been trampled over some time after their death, whereas those of *Bison*, which were prevalently broken in green state, were exposed to this damage at, or soon after death.

The taphonomic history of the fossil assemblage from layers 7–5 is partially obscured by the overprint of hydraulic winnowing, which is likely to have removed a certain amount of the original specimens. Axial bones, basipodial bones and phalanges can be consumed or otherwise destroyed through carnivore ravaging. Nonetheless, the remarkably low number of these elements in layers 7–5 correlated with the strong, significant %MAU/SWI relationships (Fig. 13), the high T/V ratio, the spatial arrangement of the specimens, with their evident bimodal

Non-carnivore- and non-hominin-derived alterations		Carnivore-derived									Hominin-derived									Totals [b]
Abras/polish.	Bites	Gastric corrosion				Gnawing				Chopping	Cut marks				Hollowing out				
Observations	Observations % to Total [c]	Observations	% to Total [a]	% to Total [b]	% to Total [c]	Observations	% to Total [a]	% to Total [b]	% to Total [c]	% to Total [c]	Observations	% to Total [a]	% to Total [b]	% to Total [c]	Observations	% to Total [a]	% to Total [b]	% to Total [c]	
–	0,2	–	–	–	–	1	1,6	33,3	0,2	–	–	–	–	–	–	–	–	–	3
1	0,4	–	–	–	–	7	11,5	33,3	1,3	–	–	–	–	–	–	–	–	–	21
1	0,2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
9	3,1	–	–	–	–	12	19,7	21,8	2,2	–	–	–	–	–	–	–	–	–	55
8	0,4	9	81,8	23,1	1,7	1	1,6	2,6	0,2	0,2	2	15,4	5,1	0,4	1	14,3	2,6	0,2	39
14	5,7	–	–	–	–	11	18	13,8	2	0,7	11	84,6	13,8	2	6	85,7	7,5	1,1	80
19	6,4	–	–	–	–	15	24,6	12,4	2,8	–	–	–	–	–	–	–	–	–	121
3	–	1	9,1	2,4	0,2	–	–	–	–	–	–	–	–	–	–	–	–	–	42
36	0,9	–	–	–	–	3	4,9	2	0,6	–	–	–	–	–	–	–	–	–	152
1	–	1	9,1	16,7	0,2	–	–	–	–	–	–	–	–	–	–	–	–	–	6
1	0,2	–	–	–	–	11	18	52,4	2	–	–	–	–	–	–	–	–	–	21
93		11				61					13				7				545 [c]

orientation and the isolated teeth, toothed mandible and skull fragments largely confined in the main chamber of the cave are compelling evidence of the effects of water disturbance (Fig. 2). All these lines of evidence considered together indicate an episode when this part of the cave was flooded. The incompleteness of all the skeletons represented at the site, included those of the bears that had died in hibernation (the biotic autochthonous constituents of a cave assemblage, sensu Simms 1994) indicates that the event occurred in a post-depositional phase; a considerable amount of the information needed to write the complete taphonomic history of the assemblage was likely lost because of this. An inflow of water also accounts for otherwise puzzling bone surface modifications, such as plat root/fungal/bacterial tunneling, which may have been acquired outside the cave, and polishing, which, when not caused by chemical action, can be due to abrasion or wear during transport. In any case, these alterations denote the presence of specimens that water introduced into the cave and that Simms (1994) classifies as abiotic allochthonous constituents.

5.2. Shed antlers

Significant biotic allochthonous constituents of Biśnik Cave's layer 7–5 are the 51 shed cervid antlers. Such a concentration of shed antlers is certainly not unprecedented. Large collections of naturally shed antlers the have repeatedly been found associated with Neanderthals of widely different age (e.g., Guado San Nicola, southern Italy: Muttillo et al., 2014; Peretto et al., 2016; Bilzingsleben, Thuringia, central-eastern Germany: Mania, 1986; Mania et al., 1994; Vollbrecht, 2000; Müller and Pasda, 2011; Poggetti Vecchi, central Italy: Benvenuti et al., 2017; Aranguren et al., 2019; Balve Cave, north-western Germany: Diedrich, 2011a, b; Raj Cave, Poland: Patou-Mathis, 2004; Oeger cave, northwest Germany: Bleicher, 1993), as well as from earlier (Erath, 1996; Becker, 2003) or even later contexts (e.g., MacGregor, 1991).

The role played by carnivores in accumulating cranial appendages in caves is controversial. Dart (1956) was perhaps one of the first to challenge the role played by hyaenas as accumulators of horns in caves. Years later, Kruuk (1972: 16) shared this opinion, based on his direct experience with modern spotted hyaenas. Guadelli (1989) had a different view about antlers, because he believed that hyaenas were responsible for the accumulation of antlers at Camiac, in France, and Stiner (1991, 1994) thought the same for the antlers accumulated in Grotta Guattari and Buca della Iena, in Italy.

From direct analysis of hyaena shelter deposits where humans were not involved, Pickering (2002) came to conclusions similar to those of Dart (1956) and Kruuk (1972) and stated that it is unlikely that hyaenas detach cranial appendages from the skulls bringing them individually from the acquisition site to the den. A few years later, Diedrich and Zák (2006) reiterated that hyaenas were accumulators of deer antlers. In their view, hyaenas were responsible for the collection of antlers in Koněprusy–Chlupáčova Sluj Cave, in Bohemia, as well as in various central European localities, among which the Perick Caves (Diedrich, 2005) and the open air site of Bad Wildungen-Biedensteg, both in Germany. Diedrich and Zák (2006) pointed out that hyaenas used antlers from *Megaloceros giganteus*, *Rangifer tarandus*, and *Cervus elaphus* as "nibbling bones" and gnawed and chewed them in most cases so intensely to leave behind only the very bases of the appendages.

Magniez (2010) examined antlers from Tournal and Portel-West, in France. He found modifications quite similar to those shown by the specimens from Camiac and from Buca della Iena and Grotta Guattari, but could not decide whether the appendages had been collected by humans or other accumulators (Discamps et al., 2011).

Using a methodology similar to Pickering's (2002), Kuhn et al. (2010) conducted an analysis of hyaena dens and found that the majority contained very low percentages of cranial appendages relative to the MNE of limb bones. The values of the horn/limb MNE ratios reported in Kuhn et al. (2010: 31) Table 8, total an average of 5,1%. Kuhn et al. (2010: 32–33) therefore concluded stating that "The data from the present study support Pickering (2002) in his rejection of the criterion that an excessive proportion of horn or antler is indicative of at least extant hyena-accumulated assemblages" and that "The current study yielded no data to lend credence to the criterion stating that an excessive proportion of horn, horn core or antler is indicative of hyena accumulations".

Addressing this topic, Diedrich (2011a, b) opposed Pickering's (2002) and Kuhn et al.'s (2010) conclusions, stating that while wolves do not actually accumulate antlers in caves, hyaenas and hominins do. According to Diedrich (2011a) the ones collected by hominins were selected purposely for tool production and are therefore larger than those gathered by hyaenas and exhibit no bite marks. Diedrich (2012) reiterated that hyaenas do collect shed antlers, but only in small amounts.

In a few tens of thousands of years after Biśnik Cave's layer 7–5, antlers had become a widespread raw material for crafting points (Clark and Thompson, 1954; Zilhão and d'Errico, 1999; Tejero, 2014). Aurignacian stone and antler points adequate for use as projectiles are in fact found not only in Europe, but also all the way down to Israel (Tejero et al., 2016; Marder et al., 2019; Orbach and Yeshurun, 2019).

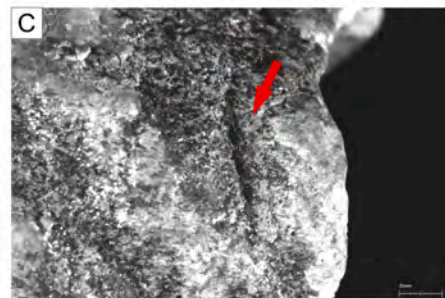Using the data in Table 3 to calculate the shed antler/limb MNE ratio
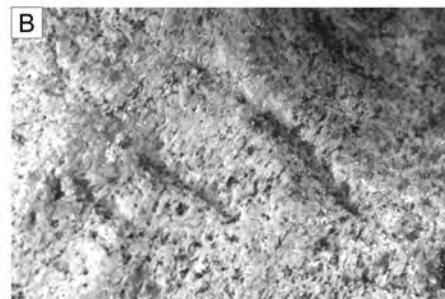
Fig. 18. Inv. nr. W/1689, *Cervus elaphus*, left shed antler, medial view. Adult individual. A) Detail of the end of the brow tine stump, exhibiting a possible tool-generated incision. Inv. nr. W/1717, *Cervus elaphus*, left shed antler, lateral view. Adult individual. B) Detail of the end of the brow tine stump, with three possibly tool-generated grooves. Inv. nr. W/1639, *Cervus elaphus*, right shed antler, medial view. Adult individual. C) Detail of the edge of the brow tine stump, exhibiting a wide, deep and relatively long scar.

(51/70, respectively) for all three the cervids represented in the faunal assemblage from Biśnik Cave's layer 7–5 we reach a total of 73%, which is much higher than the values of the horn/limb MNE ratios obtained by Kuhn et al.'s (2010). The antlers from Biśnik Cave's layer 7 are visibly damaged by carnivores and yet it is hard to believe that the carnivores, and the hyaenas in particular, invested energy into pursuing shed antlers. According to Diedrich and Zák (2006), European Pleistocene

hyaenas gnawed and chewed antlers for collagen, an opinion evidently not shared by Tejero et al. (2016: 6) who explicitly state that "antler … does not have nutritional value".

As mentioned above, Diedrich and Zák (2006) also added that hyaenas used antlers as "nibbling bones". Deprived animals were observed gnawing antlers to improve their mineral intake; among them, cervids themselves (Sutcliffe, 1973, 1977; Hutson et al., 2013). Hyaenas,
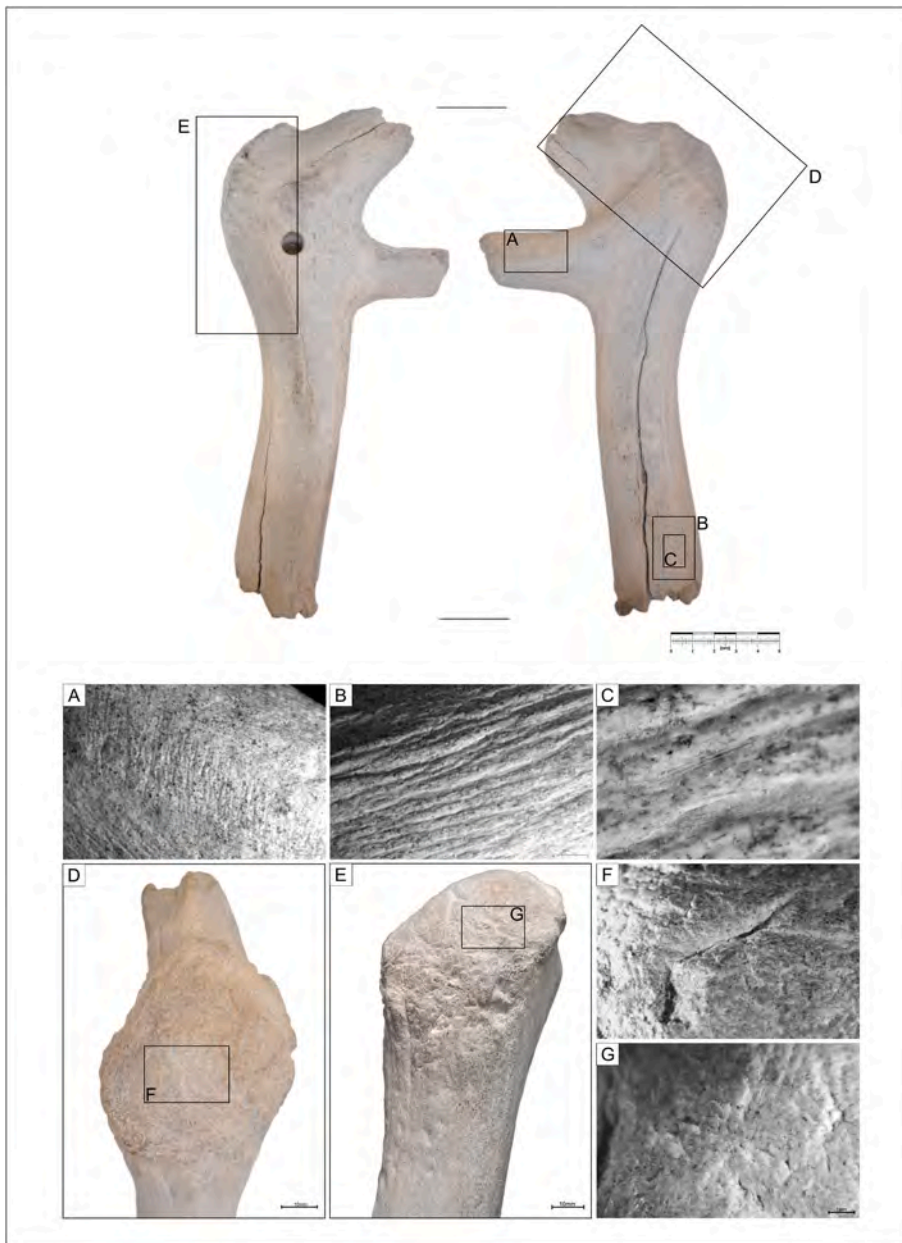
Fig. 19. Inv. nr. W/825, *Rangifer tarandus*, left shed antler. Adult individual. Upper left: lateral view; upper right: medial view; bottom left: basal view, under the burr; bottom centre: basal caudal view. A) Detail of the base of the bez tine, exhibiting grinding striations. B) Detail of the beam, showing sets of grooves parallel to the beam axis. C) Detail of B showing microstriations within the grooves. D) Detail of the burr, exhibiting use-wear marks. E) Detail of the base of the burr, showing percussion pits, cuts and scores. F) Stria under the base of the burr. G) Detail showing striae and scratches under the base of the burr.
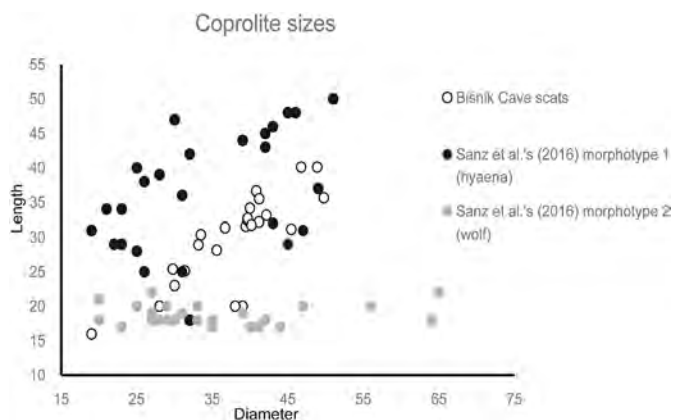
Fig. 20. Bivariate scatterplot of coprolite length versus diameter. The sizes of the coprolites from Biśnik Cave are compared with those reported by Sanz et al. (2016) for hyaenas and wolves. Measurements in millimeters.

however, are not expected to figure in this list. Matthews (1939: 47) observed that the "… faecal masses of the Spotted Hyaena … consist almost entirely of mineral matter derived from bones". Larkin et al. (2000) confirmed that, on account of the high bone content of their diet, the droppings of spotted hyaenas contain large amounts of tricalcium phosphate; chemical analyses of their faeces revealed a peak of calcium, a smaller peak of phosphorous, and a little silicon. This means that spotted hyaenas digest almost all the organic components of consumed bone. In fact, being placed at the apex of the trophic pyramid, spotted hyaenas are total consumers (Sutcliffe, 1970; Kruuk, 1972; Larkin et al., 2000). Larkin et al. (2000: 20) stated that hyaenas "will try to eat just about anything … but their diet is almost exclusively large mammals when these are in plentiful supply". Thus, it seems difficult to escape the inference that animals that are the least affected by nutritional issues and mineral deficiencies would pursue shed antlers and pile 51 of them in Biśnik Cave's layer 7. Such behaviour would also be in sharp contrast to that of their modern counterparts. Based on his direct observations of present day spotted hyaenas, Kruuk (1975: 16) reported that "only the

horns and the teeth are not eaten; hair is later regurgitated or passed with the faeces, but everything else is digested''. The cornual processes of horns grow out from the frontal bone of bovid skulls. In adult individuals, horn cores are hollow and the cavities within them are continuous with the frontal sinuses. Horn cores therefore have far higher nutritional value than antlers, which have a compact cortical bone and are densely cancellous internally. Yet, horns are left behind by famished hyaenas. Unless *Crocuta crocuta spelaea* acted very differently from modern *Crocuta Crocuta* with regards to cranial appendages (although the lack of isolated bovid horns from level 7 indicates similar behaviour of the two species), it seems illogical that highly opportunistic animals such as hyaenas would waste so much time and energy to deliberately collect and pile up anomalous amounts of antlers with very low nutritious value, simply for nibbling at, as suggested by Diedrich and Zák (2006).

In modern hyaena populations, male and low-ranking females tend to have access to low-quality food, such as bones and scraps, whereas dominant females consume better-quality food, such as meat, and generally have surplus food to carry to den-dwelling cubs (Kruuk, 1972; Bearder, 1977; Lansing et al., 2009). The presence of juvenile wolves and hyaenas in layers 7–5 (Fig. 8) indicates that the cave was a lair for these carnivores. We might therefore expect that skeletal elements associated with large amounts of useable food (meat, marrow and grease) were more likely to be transported from the kill or acquisition site to Biśnik Cave than antlers with very low nutritious value. It is hard to imagine that differential survivorship of skeletal parts can account for such an overabundance of antlers as that observed in layer 7.

Kuhn et al. (2010) gave three criteria to discriminate hyaenid from hominin assemblages: 1) a carnivore MNI ratio of ≥20%; 2) an abundance of cylinder fragments; 3) hyaena-inflicted damage upon the bones. In Biśnik Cave's layers 7–5 the carnivore MNI ratio reaches 63% (based on the data reported in Table 2), bone cylinders are merely 6.7% of the total long bones (28% of the total diaphyses), and the hyaena-inflicted damage reaches 19% in NISP counts.

Based on all these observations, considerations and results, the bone assemblage from layer 7 seems not predominantly being a carnivore-derived accumulation; hominins likely contributed substantially in forming it. At the least, hominins would have accumulated shed antlers as raw material for various possible uses. The hominid origin of the collection of shed antlers from Biśnik Cave's layer 7 could be consistent with the fact that these are the only remains from this level of the cave to display marks suggestive of hominin modifications. The shed antlers probably represented a special raw material. The systematic removal of the beam, basal tines and crown (Figs. 16 and 17) seems reflecting a habitual practice of roughing out, which apparently served to create viable shapes for subsequent use or modification. Further possible processing of the antlers may have led to the production of tools. The use-wear traces spread over nearly the entire surface of the burr and close to its base suggest that the *Rangifer* shed antler W/825 may have been hit against a hard surface, possibly stone; it is unclear whether the antler may have been used as a soft hammer. The use of antler bases as soft percussors to thin and shape stone tools has often been posited (e.g., Averbouh and Bodu, 2002; Leroy-Prost, 2002; Goutas, 2015). There are unequivocal Upper Palaeolithic hammers obtained from antlers, and pressure-flakers in bifacial tool working made from tines (Girod and Massenat, 1906; Bordes, 1974; Stodiek, 1990; Averbouh, 1999; Averbouh and Bodu, 2002; Bolus, 2003; Goutas, 2004; Bello et al., 2016). Backing up in time, Middle Palaeolithic evidence for the use of antler percussors is very scarce; early Middle Palaeolithic examples are reported from Bilzingsleben (Mania, 1986), Early to early Middle Palaeolithic ones from caves near Monaco (Breuil and Barral, 1955), and Early Palaeolithic ones from Boxgrove (UK), which date to 500 ka (Wenban-Smith, 1989; Pitts and Roberts, 1997; Roberts and Parfitt, 1999; Pettit and White, 2012; Smith, 2013; Stout et al., 2014).

Quite controversial and intriguing is the hollowing out of the inner, cancellous parts of various antlers. It is likely that these inner, more porous sections of the antlers were selectively corroded by some aggressive aqueous solution present in the cave.

That chemical corrosion can be posited to have hollowed out some of the shed antlers is for now hypothetical, but it is not so far-fetched. Corrosion is one of the most widely attested alterations observed on the specimens from layers 7–5, especially those of *U. spelaeus* and *C. lupus* (Fig. 16). It overprinted previously existing taphonomic signatures, often obscuring and perhaps also entirely obliterating them. Experimental observations indicate that exposure to alkaline pH causes desquamation and exfoliation of cortical bone surfaces, whereas teeth remain unaffected; in contrast, acid pH affects both bones and teeth (Fernández-Jalvo et al., 2002; Fernández-Jalvo and Andrews, 2016). Large amounts of specimens from layer 7–5 show various degrees of black manganese staining and coating. Manganese deposition is related to wet, mildly alkaline and oxidizing conditions, as well as to bacterial mediation (López-González et al., 2006). Hundreds of isolated and non-isolated teeth are variously coated with manganese, but none show any sign of corrosion.

6. Conclusions

Because of the impact of its inherent limitations, ensuing from the possible loss of a (large?) part of its original size, and because of the magnitude of time-averaging, the fossil record of layers 7-5 has the potential to provide information on long-term patterns and not on smaller-scale fluctuations. Despite its limitations, we can glean several substantive insights from the fossil record of Biśnik Cave's layers 7–5.

We learned that during MIS 4–3, there was a series of different occupations of the cave, by cave bears, twice (at least) by hominins, by wolves and by hyaenas. In attempt to order the occupations through time, we can try to piece together the scattered fragments of evidence. In spite of the fact that water removed part of the skeletal material that was originally preserved in the cave, but also added a few specimens from outside, the high amount of cave bear remains still present in the assemblage indicates that the cave was used, for a minimum of roughly a hundred years but more likely at irregular intervals during a far longer time period, as a lair by many generations of *Ursus spelaeus* and was a site of cumulative cave bear mortality related to hibernation. The very low evidence of carnivore-derived modifications on the cave bear bones indicates that the interactions between bears and other carnivores were rare and sporadic, and the absence of any sign of modification by man that there was none with hominins. The cave bears from layers 7–5 therefore behaved similarly to many other extinct and extant hibernating bears, reducing the risk of surprise attacks by other predators by watchfully hiding their lairs.

During the deposition of layer 7, hominins occupied the cave more or less durably, using it as a (seasonal?) shelter, but especially as a warehouse where storing naturally shed antlers which were seemingly very wanted raw material, likely for making tools from or with (as already posited in earlier contributions: Cyrek, 2003; Cyrek and Sudoł, 2010). The surprisingly high concentration of antlers in Biśnik Cave's layer 7 makes it tempting to speculate that hominins intentionally occupied the cave precisely when antlers were shed and could be collected in the area, where apparently cervids abounded. Because the majority of the antlers from layer 7 belong to *Cervus elaphus*, we can suppose that the cave was at least occupied during February–March. Antler forms an important source of mineral for various animals (cervids included, but not hyaenas, for the reasons given above) and can therefore only be found during a brief period of time during the year.

The extensive and sometimes deep bites and gnawing marks present on the antlers indicate that in the time period of accumulation of layer 7 the "antler quarry" was seldom visited by hyaenas and/or wolves in moments when hominins were not present, or was permanently occupied by the carnivores after hominins had finally left the cave. The breakage in dry state of the bear and wolf bones, the intense breakage in both fresh and dry state of the remains of *Rangifer tarandus*, and the high

incidence of trampling and prevalent breakage in fresh state of the remains of *Bison priscus* in layer 6 indicate phases of fairly repetitive and/or prolonged occupation of the cave by carnivores. Finally, layer 5 deposited during the second documented hominin occupation. Apparently, this time hominins were not aimed at gathering shed antlers, or they occupied the cave in other times of the year when shed antlers were no more available. Then, upon one of the cave's final inundations, perhaps much of what was originally contained in it was washed away.

The intriguing "antler quarry" raises a considerable number of issues. The deep scores in the peripheral areas of the antler beam and tine stumps are most equivocal and controversial and raise a number of questions. Were the cuts made to detach flakes from the compact cortical layer of the antlers? If so, what were the flakes used for?

The taphonomic analysis of the faunal assemblage from Biśnik Cave's layers 7–5 yields not only interesting new insights into the life habits of the animals represented in it, into the possible interactions between them and into the succession of pre- and postdepositional events which involved their remains. It also possibly reveals still imperfectly known technological attempts or consolidated practices, thereby providing new understandings of hominin habits at the dawn of the last glacial episode in Central Europe.

Author contributions

Paul Peter Anthony Mazza: Conceptualization, Methodology, Data curation, Investigation, Visualization, Supervision, Writing-Original draft preparation, Writing-Reviewing and Editing Krzysztof Stefaniak: Data curation, Investigation, Supervision, Writing-Reviewing and Editing Chiara Capalbo: Investigation Krzysztof Cyrek: Data curation, Investigation, Supervision, Writing-Reviewing and Editing Łukasz Czyżewski: Data curation, Investigation, Visualization Adam Kotowski: Investigation Justyna Orłowska: Investigation Adrian Marciszak: Investigation Urszula Ratajczak - Skrzatek: Investigation Andrea Savorelli: Investigation Magdalena Sudoł-Procyk: Investigation.

Data availability

Datasets related to this article are available from the corresponding author upon reasonable request.

Declaration of competing interest

The authors have no conflicts of interest to disclose.

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